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THE HIPPOBOSCIDAE OR LOUSE-FLIES (DIPTERA) OF MAMMALS AND BIRDS

PART I. STRUCTURE, PHYSIOLOGY AND NATURAL HISTORY

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(*Continued from volume XXXII*)

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NATURAL HISTORY (*continued*)

IV. Host-Parasite Relation

The preceding pages should have made it clear that every detail of the organization, physiology and behavior of the Hippoboscidae is closely integrated with a highly peculiar type of obligate and permanent ectoparasitism on warm-blooded vertebrates. The outstanding feature of these insects, which they share with only a few other Arthropoda, is that all instars of the life cycle feed exclusively on vertebrate blood, either directly or indirectly.

In the present section several aspects of this unusual host-parasite relation will be discussed on a world-wide basis, in an effort to discover general, possibly more fundamental, underlying trends. The host relations of the New World species will be examined more in detail at the conclusion of the Monograph, when it will be possible to present a comprehensive list of the American hosts and their known flies.

Much of the discussion of host-parasite associations concerns the problem of *host specificity,* sometimes called also host preference or faithfulness. This may be defined as the tendency of every parasite to choose from among the several available hosts, one or more that best fulfill its special requirements, particularly for shelter and food. It is usually a matter of degree. In the case of the hippoboscids, it must be determined almost entirely from a critical analysis of host records obtained in nature. As so much depends on the reliability of the available data, attention may be called to the pitfalls and limitations of the method.

Erroneous Records. False records, either published or found in collections, are often due to human errors, such as the wrong labelling of specimens, erroneous transcription, misunderstanding of collector's notations, and faulty memory.[17] Early describers of Hippoboscidae were often indifferent or careless in the matter of hosts. Macquart and Bigot, for instance, seldom mention them, and their type localities are also of the vaguest. A good example of an unreliable record is Denny's (1843) statement that he collected his *Lipoptena pteropi* on an East Indian fruit-bat; as no other person has seen since a hippoboscid on this or on any other bat, Denny can only have been misled by a faulty memory.

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[17] In my Monograph of the Melophaginae (1942*a*, p. 78) I wrote that winged specimens of *Lipoptena cervi* (= *Ornithobia pallida*) had been taken on an "eland," which was a slip of the pen for "elk."

Possible misidentification of either the host or the fly must be considered, as well as the troublesome matter of the synonyms of the generic and specific names of both parasite and host. The entomologist is usually forced to rely on the names of the hosts he receives with the flies; although he should attempt to correct them if they are open to question. If a museum skin of the host is made and provided with the same collector's number as the fly, the host's name can often be revised by a competent specialist. In such matters, as well as in those of vertebrate synonymy, I have been fortunate in obtaining valuable assistance from the Curators of mammals and birds in several museums here and abroad. The entomologist should not be too exacting about the labelling of specimens with host names, since he depends for so much of his material on the good will of bird and mammal collectors. For common and fairly well-known hosts, vernacular names are often satisfactory, at least in temperate regions; although such vague terms as swallow, owl, hawk, chicken hawk, buzzard, ''gavilan,'' dove, or wood pigeon are in most cases worthless. It should always be specified whether the term ''pigeon'' refers to a wild or to a domestic bird.

I have taken some pains to revise the names of the louse-flies used by previous writers and to discredit all erroneous or questionable records. It is unfortunate that so many errors have found their way even into reputable text-books, to be copied again and again. It is chiefly for the sake of accuracy that Part II of this Monograph lists all the flies I have studied personally, even when the same specimens have been recorded before in print. Moreover, all previously published records are credited to the original authors in the bibliographies of the species under the names they used. Some published host records are obvious errors, such as those of the European deer-ked, *Lipoptena cervi*, on a bracket, *Mazama*, in Uruguay (Calzada, 1939; cited by J. Bequaert, 1942*a*, p. 67), and on a deer, *Odocoileus virginianus gymnotis*, in Venezuela (Fiasson, 1943, *Rev. Sci. Méd. Pharm. Vétér. Afrique Franç. Libre*, **2**, p. 148); on a bushbuck, *Strepsiceros* (*Tragelaphus*) *scriptus*, in Portuguese Guinea (Tendeiro, 1948, *Bol. Cultur. Guiné Portuguesa*, **3**, No. 11, p. 679); and on a Grant's gazelle, *Gazella granti*, in Kenya (Lewis, 1931; cited by J. Bequaert, 1942*a*, p. 67). Cases involving the correct use and synonymy of generic and specific names are more troublesome. This problem is especially acute for the three Holarctic species of *Ornithomyia*, which were confused for many years and concerning which no full agreement has yet been reached. I regard *Ornithomyia lagopodis*, described by Sharp (1907) from European grouse, *Lagopus lagopus albus* and *L. scoticus*, as a synonym of *O. fringillina* Curtis; this opinion is not shared by some British specialists, although they agree that it is not restricted to grouse.

Contaminations. The most annoying sources of error in establishing the true hosts are the contaminations, which Hopkins (1949, p. 424) defines as occurrences of ectoparasites on abnormal hosts due to the direct, though fortuitous intervention of Man. Contamination with strange Hippoboscidae is unusually frequent, because many of them are either good fliers or active runners and promptly leave dead or even disturbed live hosts to settle later on other vertebrates. It occurs most often when freshly-killed animals of different species are carried in the same bag or box or are kept together in a room. It is much rarer later in museum collections, because dried skins of mammals and birds seldom retain flies. The only louse-flies from museum skins on record are specimens of *Allobosca crassipes* found by Ferris and Cole (1922) on a lemur skin at the U. S. National Museum, and 2 specimens of *Melophagus ovinus* labelled as taken from a museum skin of Marco Polo sheep (J. Bequaert, 1942*a*, p. 186).

Birds trapped alive, mainly by bird-banders (or bird-ringers), have furnished many and valuable host records. However, Dr. C. M. Herman (*in litt.*, 1951) cautions against a possible source of contamination in this connection. He writes that, on Cape Cod, Massachusetts, ''frequently several species of birds were in the traps together for a period of as much as several hours before being examined. This presents the chance for the parasites to get on aberrant hosts. However, in the case of the pine warblers, redwings, cowbirds, towhees, and various species of the sparrow, these were frequently captured in large numbers in the traps when no other species were present.'' Owing to the possibility of live contamination in traps, Dr. Herman is now inclined to disregard the Cape Cod records he published (1937*b*, p. 163) of *Ornithoica vicina* from the mourning dove, *Zenaidura macroura carolinensis.* Because of the ease with which flies may pass from one live host to another, little value should be attached to records from birds or mammals kept in captivity, particularly in zoological gardens. The recorded capture of *Lynchia americana* on the Mexican *Calocitta formosa*, in the Zoological Park at Washington, D. C., is a case in point.

Artificial Hosts. It is somewhat of a fad nowadays to attempt feeding all kinds of ectoparasites on laboratory animals, and rather ludicrous conclusions are sometimes drawn from such experiments. It should never be forgotten that laboratory and nature are two different types of environment. Needless to say, however interesting or valuable it may be for other purposes, mere successful laboratory feeding of louse-flies on Man, monkeys, guinea pigs, white rats, rabbits, domestic fowl, etc., has little bearing on the problems of host choice and host specificity in nature. Experiments in which the flies actually succeed in breeding on an unusual host are more interesting. Coatney (1931) kept *Pseudolynchia canariensis*, the pigeon-fly, alive in the laboratory on domestic fowl for at least 15 days, the flies producing meanwhile normal puparia from which adults later emerged. The pigeon-fly occurs sometimes as a stray on domestic fowl; it has never been able to become established on this host, in spite of many opportunities.

Stray Flies or Stragglers. I follow Hopkins (1949, p. 425) in restricting the term "straggling" to the temporary establishment of a louse-fly *under natural conditions* on an abnormal or accidental host, with the added qualification that the fly must be unable to breed on this host. Even in this narrow sense, strays are very common in the Hippoboscidae, owing to the great mobility of the adult of most species and to the fact that the puparium usually develops away from the host. A newly-emerged fly, forced to locate a suitable host at random, often reaches the wrong animal. This peculiarity of behavior is no doubt at the root of the low degree of specificity shown by many hippoboscids. Straggling may occur also later, when older flies leave a normal, dead host. Bird-flies in particular tend to leave the bird's body soon after death. Such flies often alight on the hunter or on his dog. In nature, flies sometimes pass to a bird of prey that kills the normal host, as Curtis (1836) suggested over a century ago. In discussing the phoresy of Mallophaga, I mentioned that an *Ornithomyia fringillina* taken on a vulture, *Cathartes aura teter*, in Oregon, carried several Mallophaga characteristic of fringillid birds, proving that the fly had strayed to the bird of prey from another host. Ash (1952, p. 29) found on an adult great spotted woodpecker, *Dendrocopus major anglicus*, in England, an *Ornithomyia avicularia* carrying 4 *Brüelia marginata*, a louse occurring normally on the European robin, *Turdus merula*.

Straggling usually differs from mere contamination in that the flies at least attempt to feed on the abnormal host, but the distinction is sometimes difficult for unusual records. Instances of louse-flies biting people spontaneously (outside experiments), to be discussed later at some length, should all be regarded as stray infestations, since Man never serves as a breeding host. The few cases reported by Galli-Valerio (1932) and Eichler (1939*b*) of European swallow and swift flies, *Stenepteryx hirundinis* and *Crataerina pallida*, becoming established temporarily on cage birds also belong here. The Micheners (1936) reported a similar occurrence in California, several unidentified bird-flies settling on a captive mocking bird, *Mimus polyglottos*, after leaving live wild birds that were handled in the same room.

Obvious or probable straggling under fairly natural conditions is common, as the following examples will show, assuming that none of them were due to errors or contaminations. *Ornithomyia avicularia* (possibly in some instances confused with *O. fringillina*), as a rule mainly a parasite of passerine birds, is recorded from lamb in England (Ormerod, 1900*a*, pp. 59–63; in Wallace, 1904, p. 264); from domestic fowl in England (Theobald, 1896; Wingate, 1906); from domestic pigeon in France (Railliet, 1895, p. 746); from peacock in Scandinavia (Zetterstedt, 1848); from heron in France (Charbonnier, 1912, p. 75; perhaps a misidentification); from night heron, *Nycticorax n. nycticorax,* and bittern, *Botaurus s. stellaris,* in France (Massonat, 1909); from moor-hen, *Gallinula c. chloropus*, in England (Thompson, 1937); and from curlew, *Numenius a. arquatus*, in Denmark (Johnsen, 1948). There are similar records of *O. fringillina* (= *O. lagopodis*), also chiefly a parasite of Passeriformes, from curlew, golden plover, *Pluvialis a. apricaria*, and gull, *Larus* sp., in Denmark (Johnsen, 1948); from oystercatcher, *Haematopus ostralegus*, lapwing, *Vanellus vanellus*, golden plover, and Arctic skua, *Stercorarius parasiticus*, in England (Smart, 1939); from ringed plover, *Charadrius h. hiaticula*, in England (Thompson, 1937); from curlew, in England (Ash, 1952); and from white stork, *Ciconia c. ciconia,* in Germany (Eichler, in Niethammer, 1938, **2**, p. 298). Both flies are sometimes reported from European swallows and martins, usually due to a confusion with *O. biloba*, the specific parasite of Hirundinidae. There is one reliable record of *O. biloba* straying to an eagle owl, *Bubo b. bubo*, in Belgium (Bequaert and Leclercq, 1947). *Lipoptena cervi*, the deer-ked, was taken on a nilgau, *Boselephas tragocamelus*, in an American zoological park, and on chamois, *Rupicapra rupicapra*, in Europe (Bequaert, 1942*a*, p. 72); also, in Europe, on badger, *Meles meles* (Massonat, 1908*b*, p. 617; 1909, p. 256), on horse (Mégnin, 1899; Austen, 1903), and on cattle (Kohn, 1924). Massonat's two females from a badger at Les Dombes (Dept. Ain), France, scarcely prove Hase's (1939, p. 411) surmise that the deer-ked possibly overwinters on the badger itself or in its burrows. R. Blanchard's (1890, **2**, p. 494) report of *L. cervi* from a wild boar, *Sus scrofa*, needs confirmation from a more reliable source. Most reports of newly-emerged, winged *L. cervi* from birds are imaginary or uncritical. *Lipoptena mazamae*, a native American deer-ked, was found on cattle in the United States on two occasions (Bequaert, 1942*a*, p. 129; Eads, 1949) and on a grison, *Tayra barbara*, in Ecuador (Bequaert, 1942*a*, p. 129; possibly a contamination). It is also reported from cattle in Venezuela (Gallo and Vogelsang, 1951, *Rev. Med. Veter. Paras., Caracas*, **10**, pts. 1–4, p. 35). Reported occurrences of *Hippobosca equina*, *H. variegata*, *H. camelina*, and *Melophagus ovinus* on animals other than the normal domestic hosts will be discussed later; those that are reliable were based either on strays or on contaminations. Other stragglers of American species will be mentioned in Part II.

Owing to the many possibilities of error, contamination and straggling, one should view with suspicion or disregard all aberrant host records of Hippoboscidae, at least until they are corroborated. It follows that, in this group of parasites, the so-called ''type host,'' or the species (or race) of animal from which the parasite was first described, is practically meaningless. This contention will be strengthened by a later examination of the varying degree of specificity of the louse-flies. In some respects it is fortunate that so many of the flies were originally described without mentioning a host.

Normal or Breeding Hosts. The most satisfactory test of a normal host, as distinguished from one that is only a stray or accidental, is its suitability for the continued, successful perpetuation of the parasite under natural conditions. Obviously normal reproduction is essential for species survival and any host unable to provide the parasite with the necessary food, shelter and other prerequisites for this purpose, can only be regarded as unsuitable, and hence as abnormal, accidental or temporary. Such non-breeding hosts should not be considered in discussing true host specificity, for they cannot by themselves maintain the parasitic species. A *breeding host* of a hippoboscid may then be defined as a bird or mammal which fulfills at the same time all the requirements for the normal life of the adult fly and for the continued survival of the species in nature. A satisfactory feeding host is not necessarily a suitable breeding host. In discussions of the host-parasite relation and the evolution of parasitism, too much emphasis is sometimes laid on the nutritional requirements of the individual parasite, the other less obvious factors of appropriate shelter and suitability for reproduction being minimized or even overlooked. In the Hippoboscidae, at any rate, owing to the peculiar, extremely slow mode of reproduction, adequate shelter and reproductive possibilities may be of greater importance in determining the host preference than the biochemical and other differences of the food offered by the several potential or available hosts.

Unfortunately, it is seldom possible in practice to apply the test of successful breeding to the Hippoboscidae, because the details of reproductive behavior can rarely be observed in nature. Success or failure of laboratory breeding experiments carry little weight, as it is nearly impossible to duplicate all the ecological conditions of the natural environment of both parasite and host, especially those of the nesting sites. In most cases one must rely on a critical analysis of available host records, usually obtained at random. It is of the utmost importance to gather numerous host records for each species, so as to accumulate positive evidence. For this reason I shall list in Part II of this Monograph for the American flies every locality and host record obtained either by myself or by others. If a species is reported from a given host in several localities by several observers, or repeatedly in the same locality, particularly from broods of young or juveniles, this animal may, as a rule, be safely regarded as a true breeding host. For most European and North American louse-flies the available records are now so numerous and spread over so much territory, that the breeding hosts can be recognized with fair accuracy. It is doubtful, nevertheless, that, even in these cases, the records could be studied on a percentage basis, except perhaps in a general way, such as the selectivity for families or orders. In the remainder of the World, including the West Indies and tropical America, only the barest start has been made thus far with collecting the necessary data and at most tentative conclusions can be drawn, particularly in view of the extraordinary richness of the tropical bird faunae.

Location and Selection of Hosts. Obviously the first step in selecting a host is its location by the parasite. Compared with many other permanent ectoparasites, the Hippoboscidae are handicapped in this respect, because in the majority of species the adults emerge away from the host. The completely apterous *Melophagus ovinus* of sheep and *M. rupicaprinus* of chamois are the only definite exceptions to this rule, their puparia being glued to the under wool of the host where the adults emerge. In their case the pronounced gregariousness of the hosts ensures the transfer of the keds to new and especially to young animals. In all other louse-flies, even in the subapterous or temporarily winged forms, either the gravid females leave the host for larviposition or the puparia eventually drop from the animal after being voided in the feathers or hairs. The few cases in which puparia of *Ornithoica vicina*, *Ornithomyia* sp. and *Lynchia americana* were found in birds' plumage are exceptional and possibly seasonal occurrences, probably without general bearing on the normal host location by the flies.

From present evidence newly-emerged louse-flies reach the host by their own means, either by flight or by running. No special difficulty should be encountered by most flies of birds, which deposit the larvae in or near nests or nesting sites, where nestlings or juveniles are within easy reach. Even flies emerging in the spring from overwintering puparia easily find new hosts, the same nests or sites being often used year after year, though not always by the same species of bird. This factor may have contributed to the low degree of specificity, particularly of the common flies of most passerines. Speiser (1908*c*, p. 425) pointed out that among the bird-flies the subapterous forms (*Crataerina*, *Stenepteryx,* and *Myiophthiria* with its subgenus *Brachypteromyia*) are restricted to swallows (Hirundinidae) and swifts (Apodidae), birds that return regularly to the same nesting sites and that, moreover, usually congregate in colonies. These features of the nesting behavior of the hosts no doubt account to some extent for the unusually narrow specificity of the swallow and swift flies, as well as for the loss of the power of flight by reduction of the wings in these parasites, even though they may not have been the main incentives.

Host location is more complicated for the fully-winged hippoboscids that emerge from puparia scattered at random, as is the case for most of the mammal-infesting species. Their hosts usually roam over a wide territory, although they may return to favorite feeding, drinking and resting haunts or travel regularly along definite trails. As these flies must rely mainly on flight, they are fairly good, though rather slow and jerky fliers, at least shortly after emerging from the puparia. The permanently-winged Hippoboscinae have particularly powerful wings, the membrane itself being much tougher than usual in the Diptera and besides strengthened by fine corrugations, both features protecting the wing against wear and tear in the coarse pelt of the host.

Except for *Melophagus,* the Melophaginae emerge as fully-winged, extremely active volants; but the wings are delicate and shed soon after a proper host is reached. Practically nothing is known of the behavior of the tropical species of this group. In the North American and European forms, the volants often swarm in large numbers at certain seasons, particularly in areas well populated with the hosts. They rely mainly on flight to locate a host; although Hase (1939) observed that volants of *Lipoptena cervi* crawl up objects and upon reaching the top sometimes do not fly off, but instead remain motionless, as it were ''in ambush'': holding on with the mid and hind legs, they extend the partly folded fore legs, ready to grasp any moving object that brushes against them; in this position the haustellum often protrudes from the palpi. The peculiar waiting behavior of *Lipoptena* is similar to that assumed by the larvae (or seed ticks) of certain species of ticks in search of a host.

The larviposition and puparia are as yet unknown for the subapterous Alloboscinae of lemurs and the winged Ortholfersiinae of wallabies and kangaroos. Mr. D. C. Swan, of the University of Adelaide, recently told me in conversation that he observed wallaby flies alighting on himself in a locality where the hosts were common. This suggests that the puparia are scattered at random in the bush on the ground and develop away from the host. Although the known specimens of *Allobosca crassipes,* all collected on lemurs, have only functionless wing stumps, I suspect that this species might be fully winged at emergence and so be able to find a host by flight.

After the host dies, the problem of how its flies might reach a new suitable host before perishing for want of food and shelter must often be acute. Fully-winged forms attempt to solve it by flying about at random toward any moving object. In the case of bird-flies especially, this must result frequently in landing on a species other than the one they had left and often on a stray or unsuitable host. Winged mammal-infesting flies are favored in this respect, owing to the habit of many of their hosts to live in large herds. Wingless, subapterous, and deälated flies are practically helpless and usually doomed when the host dies away from the nest or from some other suitable animal.

The flies are guided toward prospective hosts by definite sensorial responses and tropisms, which were discussed in the section on the sense organs. Just what senses come into play for this particular purpose is as yet unclear. The compound eyes and the ocelli probably register only differences in the intensity of light, such as shadows produced by a moving bird or mammal. As the organs of smell appear to be poorly developed in the Hippoboscidae, the perception of odors is probably of little use in locating a host in nature; this may be true also for the perception of heat presumably emanating from an animal. The tactile perceptions seem to be important only after the fly has reached a potential host, in helping to decide whether or not the animal is suitable as a permanent abode, mainly from the point of view of adequate shelter and a proper blood diet.

Finally, it should be pointed out once more that a bird or mammal acceptable to an individual fly, may nevertheless be unfit for the survival of the species, if the host lacks certain requirements essential for continued breeding in nature. For instance, the type of blood, though satisfactory to the fly itself, may be unsuitable for the development of the larva into a viable puparium; or the host selected by the fly may have peculiarities of ecology or behavior, particularly with regard to the nesting habits, interfering with the insect's normal reproduction.

It has been noticed that free-living as well as parasitic blood–sucking arthropods sometimes prefer or avoid certain individuals of the same host species under similar external conditions. In a recent review of this topic, Weidner (1949, p. 107) mentions that if two horses are kept together, one may carry many *Hippobosca equina* and the other none at all. Mr. H. Hoogstraal, who is investigating the populations of the several species of *Hippobosca* in northeastern Africa, informs me (*in litt.*, 1952) that at Malakal, Anglo-Egyptian Sudan, *H. variegata* is more abundant on black cattle (25 to 100 flies per head) than on white (3 to 5 flies per head).

Interspecific Competition on the Host. Frequently one individual host harbors several types of ectoparasitic arthropods which could conceivably compete for food and shelter. Among the major groups, such as the ticks, mites, fleas, biting lice, sucking lice, blood-sucking Hemiptera and parasitic flies, competition is probably slight, because of the great differences in size, relative numbers, preferred location on the host, and seasonal, ecological or even structural peculiarities. For instance, biting lice (Mallophaga) are often abundant on hosts infested with louse-flies; but as the lice are small and feed mainly on the feathers or superficially on the skin, they scarcely interfere with the flies' own needs. The great mobility of most Hippoboscidae is an additional advantage they have over other types of parasites in the choice of feeding or hiding places.

The interesting relations between the bird-flies and certain mites or lice (Mallophaga) were discussed before. The conclusion was reached that the mites are parasites of the birds as well as of the insects, and that their females attach to the latter in order to feed and oviposit. The so-called phoresy of the Mallophaga is probably an accidental association, without any definite end in view. It can hardly be called mutualistic, since it is certainly of no benefit to the fly and doubtfully so to the louse.

To what extent two or more species of louse-flies occurring on the same individual host might be in active competition, is at present difficult to evaluate. The majority of the hosts are found infested in nature with only one species of hippoboscid, even in the case of a species of mammal or bird known to be a fairly regular breeding host of two or more species of flies. Exceptions to this appear to be rather rare.

Lipoptena depressa and *Neolipoptena ferrisi* are sometimes found on the same individual deer in western North America, although one of them tends to outnumber the other. More definite information, on a statistical basis, is desirable in this case. In North America also, *Ornithomyia fringillina* and *Ornithoica vicina* occur sometimes together on the same passerine host. At Demarest, New Jersey, of 26 trapped passerines found infested with these flies by Mr. B. S. Bowdish, in July and August, 1948, 4 birds carried both species, namely two blue jays, *Cyanocitta c. cristata,* one tufted titmouse, *Baeolophus bicolor,* and one rose-breasted grosbeak, *Hedymeles ludovicianus.* In 1950, of 50 infested trapped birds belonging to 13 species, 36 carried *O. fringillina* only, 12 *O. vicina* only, and 2 both species. *Lynchia americana* is sometimes associated with *Ornithoica vicina* on owls, or with *Ornithomyia fringillina* on game birds. Johnson (1927*a,* p. 15; 1927*b,* p. 33; 1929, p. 52) reported a heavy infestation of a great horned owl, *Bubo v. virginianus,* in Massachusetts, with at least 19 *L. americana* and 32 *O. vicina.* Double infestations involving *O. vicina* are possibly fairly common, but owing to its small size this fly readily escapes detection. Perhaps more careful investigations of live birds may show that in such cases each species of fly selects a different area of the plumage.

In Europe, the two closely allied species of *Ornithomyia, O. avicularia* and *O. fringillina,* infest much the same species of birds, as a comparison of their host lists shows; although *O. fringillina* seems to occur on a few birds that are avoided by *O. avicularia.* Nevertheless, double infestations by these flies are rare. For instance, of 120 individual birds found infested with *Ornithomyia* by Thompson (1937*a,* 1938*b,* 1940) at several British localities, only one showed a mixed infestation (1 *O. avicularia* and 3 *O. fringillina* on a British robin, *Erithacus rubecula melophilus*). Ash

(1951), who collected 41 *Ornithomyia* from 34 migratory birds of 15 species in southern Sweden (Oeland), found only one mixed infestation (with 3 *O. avicularia* and 1 *O. fringillina*) on a juvenile sparrow hawk, *Accipiter nisus.* As 7 other trapped sparrow hawks examined by Ash carried only *O. avicularia* (12 flies in all), I suggest that the single *O. fringillina* from this host may have been an accidental straggler or even a live contamination due to the trapping manipulations.

Mixed infestations are perhaps most frequent when two highly specific flies select the same type of host. Mr. I. B. Tarshis informs me (*in litt.*) that, during the summer of 1952, in an area of California where *Stilbometopa impressa* and *Lynchia hirsuta* were common on California quail, *Lophortyx californica,* of 194 infested birds, 59, or 36.4 per cent, harbored both species.

So little attention has been paid thus far to multiple infestations by Hippoboscidae, that the meagre available data warrant no further discussion of their possible bearing on the problem of active competition on the host.

Population Dynamics. It is now generally recognized that a biological species consists of a number of natural aggregates of individuals, or populations, genetically related and capable of normal and successful interbreeding within certain qualifications. Latterly the term ''deme'' has been proposed for such natural interbreeding populations making up a species or its subdivisions. From this point of view the problems of host-parasite relation and particularly of specificity should be regarded as due to the interaction of populations of parasites and of hosts. They can be properly understood only through a study of the dynamics of both.

The population dynamics of the vertebrate hosts are clearly outside the scope of this work, even if the writer were competent to discuss them. I venture to remark, however, that except in a very few instances, they are too little known to be of much help for our purpose.

The introductory remarks of this section called attention to the difficulty of obtaining adequate and reliable data on the true host relations of the Hippoboscidae. Under the circumstances it might well seem hopeless to undertake an analysis of the hippoboscid populations, which should necessarily be based on numerous observations. Not much can be attempted at present beyond discussing briefly a few of the more satisfactory cases and suggesting possible profitable lines of research.

Emphasis should be placed, of course, on the true breeding hosts, which alone maintain the interbreeding population of the parasite in a given area. Occurrences on accidental or abnormal hosts in nature should not be completely ignored, however. Stray flies carried to new territory, even by a temporary host on which they are unable to perpetuate the species, may conceivably find there another new suitable host. No doubt most of such chance introductions go to naught. For instance, *Olfersia spinifera,* a highly specific fly of man-of-war birds (species of *Fregata*) in tropical seas, was taken on one occasion in central France on one of these birds that had wandered far from its normal range; but the fly never became a permanent member of the Central European fauna for want of an appropriate host. Nevertheless, the very wide present-day distribution of certain flies, such as *Ornithomyia fringillina, O. avicularia, Ornithoica confluenta,* and *Lynchia albipennis,* might be due in part to such occasional waifs. Birds that are gradually extending their range by natural means are worth watching for possible permanent introductions of parasitic flies. During the past 25 years the eastern turkey vulture, *Cathartes aura septentrionalis,* has been moving steadily northward in the eastern United States, being now a summer breeding bird as far north as New York and Connecticut. Farther south this bird is commonly infested with *Olfersia bisulcata,* a specific parasite of the Cathartidae. It will be interesting to see whether this bird-fly will eventually become established in the new northern territory.

As pointed out before, the host itself is the most effective natural enemy limiting the louse-fly population and maintaining it normally in a state of equilibrium. The ability of the host to cope with its ectoparasites is therefore a potent factor in the population dynamics of the flies. Certain types of hosts are naturally handicapped in the constant struggle against their pests, either by a large body size or by structural features interfering with the capture of small or swift parasites. The large body size of the host may account in part for the average heavier fly infestations of many mammalian and even of certain avian hosts (vultures, owls, etc.), since it provides for more extensive feeding areas and a greater supply of blood, as well as for better hiding places out of the host's reach. Likewise, the long, thick and dense plumage and, even more so, the broad, short, clumsy and sometimes hooked bill of certain birds may interfere with their preening activity, particularly if a short neck allows little freedom of movement to the head. Such structural peculiarities possibly explain why diurnal and nocturnal birds of prey, nighthawks, swallows, swifts and similar birds frequently harbor larger fly populations than most passerines.

The degree of specificity of the parasite also influences its abundance on the host. As the reproductive potential of all Hippoboscidae is very low, it is to be expected that the relatively few adults produced within a given period will be widely scattered if the species has a great variety of suitable hosts, this being the rule for the more common bird-flies of northern temperate regions, such as *Ornithomyia avicularia* and *O. fringillina.* On the other hand, the offspring of flies restricted to one or a few species of hosts will be more concentrated, causing heavier individual infestations as well as a higher percentage of infested individuals. A good example is *Olfersia bisulcata,* which breeds only on the Cathartidae, but infests usually most of the vultures in a locality and occurs often in some numbers on individual birds.

Another natural factor regulating louse-fly populations to some extent is the degree of gregariousness of the host. Hosts which live singly or in pairs and breed in relative isolation, as a rule show very low fly infestations; while those that congregate in herds or flocks or breed in densely populated rookeries, almost invariably are heavily infested. Even among the flies of mammals, the light and rather scattered infestations of *Echestypus* on the smaller, more solitary African antelopes contrast with the heavier infestations of *Lipoptena* and *Melophagus* on other more gregarious Artiodactyla. The unusual abundance of bird-flies on swifts, certain swallows and marine birds is doubtless correlated with the gregarious habits of the hosts. Moreover, any abnormal or periodic fluctuation of the host's population influences that of the parasite. For instance, Robinson (1916) noted that in Lancashire, England, the number of nesting house martins, *Delichon urbica,* had been decreasing steadily for some 15 to 20 years prior to 1914, their parasite, *Stenepteryx hirundinis*, being also scarce during that period (usually 1 or 2, at most 3 flies per nestling). In 1915 and 1916, however, there was a large increase of nesting martins and their parasites were then more numerous than ever, it not being unusual to find up to a dozen flies on each nestling.

Obviously any abnormal impairment of a host's cleaning activities, either by very young age, malnutrition, injuries or disease, may increase its population of ectoparasites. In Germany, Ploch (1936) counted over 100 bird-flies of an undetermined species on a young disabled jay, *Garrulus glandarius;* Eichler (1939*b,* p. 220) mentions that O. Heinrich saw a sick hooded crow, *Corvus corone cornix*, near Berlin, infested with many undetermined bird-flies.

It may be difficult sometimes to decide whether the flies are responsible for the weakened condition or have merely taken advantage of it. Possibly the mere process of domestication also results in a greater individual tolerance toward ectoparasites or increases the parasitic population in other ways. As shown below, *Pseudolynchia canariensis* is often very abundant in pigeon lofts; whereas it is rather scarce on its Old World wild hosts. Heavy louse-fly infestations are more frequent on domestic sheep, goats, equines, camels, and cattle; in their case there are no comparable data from wild hosts. Zacharias (1928, p. 679) relates that he could not find *Hippobosca equina* on horses in Germany in 1927; but he was told that the fly was common on ill-fed horses shortly after the war of 1914–1918.

The study of an ectoparasitic population involves four distinct problems. It should consider first the *density of infestation*, or the minimum, maximum, and average numbers of the parasite present on individuals of a host species. Next comes the *frequency of infestation*, or the proportion of individuals in the local population of each host species infested with the parasite. The *total parasite population* of a given territory might then be determined by combining the density and frequency of infestation of all its potential host species. Obviously this presupposes at the same time a reasonably complete knowledge of the *host range* of the parasite, that is, the several species of animals it could use as either breeding or temporary hosts. In the case of the Hippoboscidae, it is doubtful that we are sufficiently informed on the density and frequency of even the most common species, although we are fairly well acquainted with their host range.

The frequency and density are most easily determined for the hippoboscids of mammals, which are more accessible and as a rule more abundant than those of birds (particularly the keds or Melophaginae of the Ungulates). Whether their heavier infestations are due in part to a higher innate rate of reproduction is open to question. I have mentioned several other, purely environmental factors which might be involved, such as the larger size of most mammalian hosts. Most mammals may also be more lax than the average bird in controlling excessive infestations, which factor may increase the average life expectancy of the female flies and hence the offspring produced over a given period.

Melophagus ovinus. Ked infestations are as a rule heavy and occur on all sheep of the flock; but few actual counts or computations have been made of the keds present. MacLeod (1948), in England, made live counts of keds and puparia by going over the whole fleece thoroughly. Checks made by counting the dead keds removed after dipping the same animals in a quick-acting insecticide, showed that the method is reasonably reliable for the adults, but not for the puparia. In two counts at an unspecified season, a first lot of 20 sheep gave a live count of 1551 adults, or about 77 per head; the second lot of 10 sheep gave 690 adults, or about 69 per head. Two other live counts were carried out in April: the first, on 10 sheep, gave 672 adults, or about 67 per head (maximum, 117; minimum, 23); the second, on 7 sheep, gave 330 adults, or about 47 per head (maximum, 68; minimum, 26). Unfortunately the size or weight of the animals is not given, although the counts were evidently made on full-grown sheep. It is rather surprising that the total adult ked population of a sheep was not larger than these counts indicate.

Lipoptena cervi. Darling (1937), referring to the occurrence of this ked on red deer, *Cervus elaphus*, in Scotland, writes: "On stags shot in October and hinds in December and January, and on occasional beast found newly dead in March, I have found hundreds and even thousands of these parasites." In view of the results of actual counts of sheep-keds, one is justified in being sceptical about such estimates, which are probably exaggerated. The only more precise information I could find is a statement by Springholtz-Schmidt (1937, p. 138) that in eastern Siberia sometimes up to 500 *L. cervi* occur on one deer.

Lipoptena depressa. Cowan (1943, p. 186), in British Columbia, estimated that a single black-tailed deer, *Odocoileus hemionus columbianus,* might carry from 2000 to 2400 *L. depressa.* This was calculated from observing 2 keds per square inch of body surface on a deer with a body area of between 1000 and 1200 square inches. It is doubtful that this method is reliable, since it is improbable that the density of the population is the same over most of the body. Cowan also states that of 42 deer examined on Vancouver Island, only two were free of keds, one in December and one in January. Dixon and Herman (1945, p. 9) actually counted a mixed population of 1350 *L. depressa* and *Neolipoptena ferrisi* on one mule deer, *O. h. hemionus,* in California. These authors observed that in heavy infestations the keds are sometimes attached to one another, as many as 7 in a chain.

Lipoptena mazamae (= *L. depressa* var. *mexicana*). Townsend (1897, p. 289) found 153 specimens on one Mexican white-tailed deer, *Odocoileus virginianus mexicanus,* in Vera Cruz, Mexico.

With some striking exceptions to be mentioned below, the bird-fly populations usually show a low density and frequency. The flies are often more abundant on young nestlings than in general on adult birds, particularly brooding parents. The nestlings are more accessible to flies emerging from puparia in or near the nest and are more helpless or less efficient in controlling their ectoparasites. When the young are disturbed, the flies can hide beneath them or in the nesting material. Meanwhile the brooding birds provide the proper temperature and humidity and will scarcely attempt to destroy flies on their offspring. Even after leaving the nest, fledglings and juveniles are usually more heavily infested than the older birds.

Ornithoica vicina. The breeding hosts of this common American fly belong to two unrelated orders. They include first a variety of Passeriformes (58 species known at present in North America), on which the infestations are usually light, often one and rarely more than 2 or 3 flies being present on one bird. According to Herman (1937, p. 163), on Cape Cod, Massachusetts, various fringillids are most abundantly infested, particularly the song sparrow, *Melospiza m. melodia,* which often carries 6 to 8 flies. An exceptional case was a redwing, *Agelaius p. phoeniceus,* captured alive by itself in a trap and which harbored 19 flies. During one trapping season at Demarest, New Jersey, Mr. B. S. Bowdish collected 1 or 2 *O. vicina* per bird from 9 specimens of 5 species of passerines. *O. vicina* is also a frequent parasite of Strigiformes, on which it is as a rule more abundant than on the passerines. Johnson (1927) reported 32 specimens taken late in September from one great horned owl, *Bubo v. virginianus,* at Wenham, Massachusetts. On August 16, 1944, H. D. Fisher collected 42 flies from one screech owl, *Otus asio kennicotti,* at Departure Bay, British Columbia.

Ornithomyia avicularia and *O. fringillina.* Ash (1952) published a summary of his captures of these two flies in one locality of Berkshire, England. He examined in all 30 broods of 16 species of birds, 149 juveniles of 14 species, and 15 adults of 11 species, between June 18 and the end of October, 1950 (except for the period from August 24 to September 19). Of the 24 species, 11 were free of flies (9 Passeriformes, 1 Falconiformis, and 1 Strigiformis) and 13 infested (10 Passeriformes, 2 Piciformes, and 1 Strigiformis). Of the 30 broods examined, 5 belonging to 3 species were infested; of the 149 juveniles, 60 belonging to 9 species carried flies; and of the 57 adults, 20 belonging to 7 species had flies. If each brood is counted as one individual host, 37.1 per cent of the total birds examined carried flies; and of the infested birds 6.2 per cent were broods of young, 71.6 per cent juveniles and 22.2 per cent adult birds. In the same paper Ash reports counting at least 24 *O. avicularia* on a brood of 3 nestlings of the green woodpecker, *Picus viridis,* 10 *O. fringillina* (as *O. lagopodis*) on a curlew, *Numenius arquatus,* and 50 *O. fringillina* (as *O. lagopodis*) on a juvenile Montagu's harrier, *Circus pygargus.* In an earlier paper (1950), he mentions taking about 60 *O. fringillina* (as *O. lagopodis*) from one brood of nestling merlins, *Falco c. columbarius,* in Co. Durham, England. It is noteworthy that none of these unusually heavy infestations were from passerines, the more normal breeding hosts of these flies, but from birds mostly provided with bills ill-adapted to catching ectoparasitic flies. In a series of about 160 British birds, infested with either *O. avicularia* or *O. fringillina,* belonging to 35 species (17 Passeriformes, 1 Piciformis, 1 Cuculiformis, 3 Strigiformes, 2 Falconiformes, 3 Galliformes, 1 Columbiformis, and 7 Charadriiformes), examined by Thompson (1937*a;* 1938*b;* 1940), the majority (106) each carried one fly only; a moderate number (33) had 2 flies and few more than 2 (14 with 3 flies; 2 with 4; 2 with 5; 3 with 6). An unusual case was that of a grouse, *Lagopus scoticus,* infested with 11 flies, although the usual number for this bird is 1 or 2. Some of Thompson's data (1940) are based on flies taken by Mr. Arnold Clark in Kent, England, from trapped live birds in one season: of 112 birds (43 adults and 69 juveniles) in this lot, belonging to 7 species of passerines, 61, or about 55 per cent, were infested; of these, 7, or 11 per cent, were adults and 54, or 89 per cent, juveniles. A few individual birds were caught on more than one occasion in the trap and some of these had acquired flies meanwhile. Marples (1935), also in England, found *O. avicularia* on each of over 30 trapped live robins, *Erithacus rubecula melophilus,* with one exception; 28 birds carried only one fly each and one bird had 2 flies. Reference will be made later to Ash's (1951) observations of the incidence of *Ornithomyia* on migratory birds in Sweden.

There are as yet no strictly comparable data concerning the incidence of *Ornithomyia fringillina* on North American birds, information on the frequency of infestations in the general bird population being particularly scant. Certain passerines are clearly preferred to others. According to Dr. C. H. Herman (1937*b,* p. 164), on Cape Cod, Massachusetts, live cowbirds, *Molothrus a. ater,* trapped in August, were rarely without at least one fly; 10 to 20 flies per bird were common occurrences and one of them carried as many as 23. Redwings, *Agelaius p. phoeniceus,* were almost as abundantly infested as cowbirds. During the period of study (1936 and 1937), *O. fringillina* was obtained from 16 other species of birds, but in small numbers, nearly always from adults and juveniles. The only case in which it occurred on nestlings was on 2 cowbirds from the nest of a chickadee, *Penthestes a. atricapillus.* A single *O. fringillina* was found in the feathers of this adult chickadee when it was captured on the nest a few days later. Since several other chickadees examined were not infested, Herman surmises that this bird is an abnormal host and that the one with a fly had acquired it through the parasitic nesting habit of the cowbird. At Demarest, New Jersey, Mr. B. S. Bowdish found from 1 to 4 *O. fringillina* on each of 37 passerines of 13 species during the 1950 trapping season (31 with 1 fly, 3 with 2 flies, 2 with 3, and 1 with 4); in 1947, 24 passerines of 11 species carried each from 1 to 3 flies (20 with 1 fly, 3 with 2 flies, and 1 with 3). In Ontario, C. H. D. Clarke took 4 flies from a young evening grosbeak, *Hesperiphona v. vespertina,* being fed by the mother.

At Groton, Massachusetts, Wharton (1933, p. 109) banded 2752 trapped birds of 68 species during the three years 1929 to 1931. Of these only 141, or 5.1 per cent, of 11 species, carried hippoboscids, either *Ornithomyia fringillina* or *Ornithoica vicina.*

Stenepteryx hirundinis. Eichler (1942*b,* p. 6) reports that near Göttingen, Germany, this fly was common in all colonies of nesting house martins, *Delichon urbica,* usually only a few flies on each bird, the maximum being 12 on one nestling. Robinson's (1916) observations on the variation in the density of this fly have been quoted before in the general discussion of the factors influencing the dynamics of populations.

Crataerina pallida. This fly is often abundant in the nests and on the adults of its normal host, the European swift, *Apus apus.* It is an outstanding example of the influence of host gregariousness on the size of hippoboscid populations. Giebel (1867) collected 24 flies from a dead adult swift near Wittekind, Germany; he referred them to *Stenepteryx hirundinis,* but they were certainly *C. pallida,* as Brauer (1868, *Arch. f. Naturgesch.,* **34**, pt. 2, p. 483) pointed out. Fallou (1871) noted from 15 to 20 *C. pallida* on a number of *Apus apus* found dead in the streets of Paris following the riots of 1871. Büttiker (1944), in Switzerland, found 24 *C. pallida* on 3 nestlings of *Apus apus* in 1941, about 40 on 7 nestlings in June, 1942, and 10 on 7 nestlings in July, 1942; on the other hand he took only 2 and 7 flies respectively on 2 adult swifts killed accidentally. Klůz (1950, pp. 48 and 51), in Czechoslovakia, observed

2 to 6 flies on adult brooding swifts, but many more on the young nestlings (as a rule 7 to 12, rarely 16, 18, 21 and even 26 on one nestling). Kemper (1951, p. 227), in Germany, found flies on adult swifts in June and July, on the average 3 flies per bird, the largest number observed being 11 on one swift.

Stilbometopa impressa. This fly seems to be common on at least two species of quail in the western United States, but particularly on the California quail, *Lophortyx californica.* Herman (1945, p. 21) states that as many as 10 flies were collected from a single bird. Tarshis (1952, p. 78) mentions taking close to 1600 adult flies from trapped quail in California between 1946 and 1951.

Lynchia americana. This common North American fly has a wide range of breeding hosts in the three Orders Falconiformes, Strigiformes and Galliformes. On most of them the infestations are light. On others they may be very heavy and this seems to be often the case on owls, as has been repeatedly observed. I reported (1945*a*) that Dr. C. E. Palm collected from a great horned owl, *Bubo v. virginianus,* near Ithaca, New York, on August 28, 61 flies, several more escaping. I owe to Mr. E. K. LeDune, of the New York State Conservation Department, valuable information on the frequency of *L. americana* on ruffed grouse, *Bonasa umbellus,* in that state. Of 147 juvenile birds examined for ectoparasites during 1935 and 1936 (from June 8 to August 29), 32, or 21.7 per cent, were fly-infested, as follows: 4 birds with 1, 6 with 2, 12 with 3, 7 with 4, 4 with 5, 2 with 6, 1 with 7, 1 with 8, 2 with 10, 1 with 12, and 1 with 15 flies.

Lynchia fusca. Herman (1945, p. 22) reports that as many as 18 of these flies were taken from a single great horned owl, *Bubo virginianus pacificus,* in Lassen Co., California.

Lynchia dukei. G. H. E. Hopkins collected 10 specimens (8 ♀ and 2 ♂) on one fishing eagle, *Haliaeëtus vocifer,* in the Kazinga Channel of Lake Edward, Uganda, on June 30, 1934.

Lynchia hirsuta. California quail, *Lophortyx californica,* are commonly infested with this fly, Tarshis (1952, p. 78) reporting that he took nearly 1000 adult flies from trapped birds from 1941 to 1951.

Several of the species of *Olfersia* occur as heavy individual infestations on a large proportion of their preferred breeding hosts. This is especially true of species living on young marine birds that nest in rookeries, such as *O. aenescens* and *O. fossulata;* also, but to a lesser degree, of *O. bisulcata* of the American vultures (Cathartidae).

Pseudolynchia canariensis. Schuurmans Stekhoven and his coworkers, at Tucumán, Argentina, found that in the pigeon lofts the squabs carry on the average more flies than the adults (unpublished observations). The numbers varied from 1 to 20 flies per squab; sometimes when 2 squabs were present in one nest, one carried more flies than the other. If a squab was freed of flies and left in the same nest, it became rapidly reinfested. In one case a squab was freed of all of 5 flies on August 24, again on August 25 of 1, on August 27 of 4, and on August 29 of 2 flies. Very young squabs, almost without feathers, may be infested, and copulating pairs were also found on squabs. According to Kartman (1949, p. 127), at Honolulu, Hawaii, both juvenile and adult domestic pigeons were generally infested, 50 juveniles averaging 2 flies per bird and 100 adults averaging 1.3 flies per bird. He noted that the major infestations were on young pigeons between 15 and 25 days of age.

Microlynchia pusilla. This fly is often taken on the mourning dove, *Zenaidura macroura,* on which it appears to be more abundant in the southern United States than farther north. Brennan (1938) found near San Antonio, Texas, nearly every one of two or three dozen doves killed infested with up to 10 flies on each bird. On the other hand, H. E. McClure (*in litt.,* 1940) reports that in Iowa he found the fly on only 7 out of some 2000 birds he examined.

It has been suggested (Kartman, 1950) that an ectoparasitic species might be regarded as a series of populations of freely interbreeding individuals each confined to an individual host, on which each population is isolated more or less as in a geographical area. Although such populations may be in frequent contact, thus allowing some inter-host migration, in many cases the physiological and morphological peculiarities of the host, together with its complex of habit patterns, are important factors influencing each parasite population. This concept can scarcely be applied to the Hippoboscidae, where in most species an individual host has very little influence on the fly population as a whole. As we have seen, under natural conditions the individual density of the flies is usually very low, except for some of the deer-keds and certain flies of marine birds, owls, swifts and swallows. In most cases a host carries only one or a very few flies, scarcely enough to function as an interbreeding population. Moreover, as the majority of the Hippoboscidae are active fliers and as, with very few exceptions, the pupal development occurs away from the host, there is practically no individual isolation of successive generations. These peculiarities of their population dynamics explain why the Hippoboscidae show little tendency toward developing races or subspecies, in spite of the very wide host range of many of the species.

Seasonal Fluctuations. Brief mention has been made of certain variations of the hippoboscid populations, mostly in response to the dynamics of the host populations. Other, definitely seasonal fluctuations, correlated with periodic climatic changes or with the migratory habits of the hosts, deserve to be considered more in detail.

It should be repeated that the Hippoboscidae are essentially tropical and subtropical insects, usually little influenced by seasonal climatic variations which in the Tropical Zone concern mainly the rainfall or the atmospheric humidity. Information is practically lacking on the seasonal incidence of tropical louse-flies; but it is reasonable to surmise that their rate of reproduction and the size of the populations remain fairly uniform throughout the year. While investigating the seasonal abundance of blood-sucking flies in a wooded savanna area of central Tanganyika, Glasgow (1946) found that *Hippobosca longipennis* was regularly attracted by a bait ox led over the bush trails, the numbers caught being about the same the year round; although in this area the dry and wet seasons are sharply marked, all the rain falling between December and April. In the author's opinion (p. 96), the slight variations in catches were presumably reflections of the movements of wild felines, the normal local hosts of *H. longipennis*.

As is to be expected, seasonal fluctuations have been investigated mainly in the Temperate Zone of the Northern Hemisphere, where all forms of life are conspicuously affected by the low winter temperature. Considered as a whole, the hippoboscid fauna of the Palearctic and Nearctic Regions comprises four elements. (1) A relatively small number of accidental stragglers from the tropics, usually brought in by casual bird visitors. Such are, for instance, *Lynchia albipennis* (= *L. ardeae*) in the British Isles (Hallett, 1932; Collin, 1932; O'Mahony, 1940), *Olfersia spinifera* (= *O. courtilleri*) in central France (Courtiller, 1853), and *Stilbometopa fulvifrons* in the United States. Obviously such flies do not concern us further. (2) Parasitic flies of domesticated mammals and birds, presumably introduced at one time by Man with the hosts. (3) Tropical or cosmopolitan species, which either normally and regularly invade more northern areas on their migratory hosts or have become more or less established and autochthonous, at least in the warmer temperate areas. (4) Strictly precinctive flies of the northern temperate regions, which seem to avoid the tropics.

The fluctuations of the flies of domestic animals are no doubt of practical importance in the control of these pests. It is doubtful, however, whether they can teach us much about the effects of the seasons on natural hippoboscid populations, even though the parasites often remain established on the hosts gone feral. I have mentioned, in connection with other topics, some of the observations made on the seasonal fluctuations of *Melophagus ovinus* (particularly those by MacLeod, 1948, in England), *Hippobosca equina* (Roberts, 1925, in England), and *Pseudolynchia canariensis* (Schuurmans Stekhoven and co-workers, in Argentina). In these flies the adult population is as a rule maintained on the host throughout the year; it builds up rapidly in spring and early summer, tends to decrease again during late summer and fall, particularly if these are dry, and is at its lowest ebb in winter. In the case of *M. ovinus,* it was also observed that in hot weather the keds migrate toward the outer areas of the fleece, which allows them to pass by direct contact from the older to the younger sheep, the only effective transfer method for this wholly apterous and clumsy fly. This combination of factors explains the frequently observed decline of the ked populations on older sheep during the summer (MacLeod, 1948; Evans, 1950). It is a more logical explanation than a supposedly acquired individual resistance to the parasite by the older hosts.

Groups (3) and (4) comprise the only hippoboscids which strictly speaking are part of the native fauna, being established permanently and by natural means. Their number is always small in any one locality or limited area of the northern Temperate Zone and tends to increase as one travels south. In the Palearctic Region, 5 species are native in the British Isles, Sweden, and Denmark; 6 in Finland, Germany, the Netherlands, Belgium and northern France; 8 in Switzerland; and 12 in central and southern France, Spain and Italy. Several tropical species, such as *Ornithoica turdi, Ornitheza metallica,* and *Pseudolynchia canariensis* (on wild hosts), invade the southern Palearctic areas, or Mediterranean Subregion. Others, such as *Ornithomyia avicularia, Lynchia albipennis,* and *Olfersia fumipennis,* which are likewise widespread in the tropics, extend even to the northern Palearctic areas. This intrusion of tropical or cosmopolitan elements is more pronounced in the warmer parts of the Nearctic Region. The peculiar features of the hippoboscid fauna of America north of

Mexico will be analyzed more in detail in Part II of this work. Neglecting 3 introduced flies, the North American fauna now comprises 26 Hippoboscidae; only 12 of these are known from the Dominion of Canada. Of the 26, 7 do not occur in the New World tropics and should be regarded as Nearctic endemics, although one of these is also Palearctic. One more is clearly an accidental waif from the Neotropics. The remaining 18 species occur in both the Nearctic and Neotropical Regions: 8 are American tropical flies which usually are not found much beyond the southern half of the United States, although they may stray occasionally farther north, particularly along the Pacific Coast; 7 extend over most of the New World, nearly all of these occurring in Canada; and 3 are more cosmopolitan, being found both in the Old and the New World, notably in the tropical areas.

The foregoing outline brings out the composite nature of the northern temperate hippoboscid faunae and explains why the flies use a variety of methods to survive the cold season. It is especially important that the tropical or more cosmopolitan flies form a substantial part of these faunae. Their survival in winter should not be too difficult, since their migratory hosts may become reinfested from other local hosts in the southern winter quarters before returning north. Some of these species no doubt survive also on permanent resident birds, particularly in the southern temperate areas. Unfortunately, there is as yet little precise information on the seasonal fluctuations of these widespread species.

Microlynchia pusilla is fairly typical of several bird-flies found both in the tropical and temperate parts of the New World. It occurs over most of South and Central America and extends in the United States as far north as Idaho, Iowa and North Dakota. In the eastern United States it is known only from Florida and it has never been taken in Canada. Its chief winter quarters are no doubt the Neotropics; there is evidence that the adults survive the winter also in the southern United States. It was collected in some numbers in Texas, during the first half of January, on the roadrunner, *Geococcyx californianus,* the bobwhite quail, *Colinus virginianus,* and the mocking bird, *Mimus polyglottos,* all three permanent residents of the southern United States. Herman (1945, p. 22) saw a female of *M. pusilla* from a mourning dove, *Zenaidura macroura marginella,* taken at Brawley, California, on April 7.

Ornithoica vicina, another American fly with a wide geographical and host range, shows some unusual seasonal features. It seems to be equally abundant in the Nearctic and Neotropical Regions and extends into Canada. Its host list is extensive, as it has been taken in the Nearctic Region on 69 species of 7 orders and in the Neotropics on 36 species of 8 orders; but the majority of these birds are either Passeriformes (58 Nearctic and 15 Neotropical) or Strigiformes (8 Nearctic and 6 Neotropical), which are possibly the only true breeding hosts. In the Nearctic Region, many of the passerine hosts of *O. vicina* are the same as those of *Ornithomyia fringillina,* and the fluctuations of the populations are to some extent similar for these two species. *O. vicina* differs, however, in that it uses in addition owls for breeding purposes, birds which frequently are northern winter residents or do not migrate very far. As in the case of *Lynchia americana,* the adults of *O. vicina* may remain on these birds throughout the winter, possibly reproducing meanwhile even in the northern areas. Thus the owls could act as temporary reservoirs for the fly, from which it could spread in the spring to passerine or other migratory birds. The seasonal frequency of *O. vicina* in the Nearctic Region is insufficiently known; the fly is common during June, July, August and September, and there are several records in October. It was taken on November 4 in Maine from a Canada jay, *Perisoreus canadensis,* a winter resident bird in that area (Johnson, 1922, p. 80), on November 7 in Pennsylvania, and on November 15 from a short-eared owl, *Asio f. flammeus,* in Ohio.

The hibernation of the relatively few strictly endemic flies of the northern Temperate Zone offers more interesting problems.

The northern deer-keds remain on the hosts throughout the winter, when mating and larviposition continue, though no doubt at a slower pace. The puparia, which eventually drop out of the pelt, remain dormant until spring, so that the adult ked population necessarily declines on the host, accidental losses not being replaced by newly-emerged flies. Meanwhile, puparia steadily accumulate in the winter haunts of the hosts. With the first warm spring days the winged adults emerge, often in great swarms. Hare (1945*a,* p. 50) noted for *L. depressa* that in the Berkeley Hills, California, no volants could be found during January and February. From the middle of March onward they appeared in ever-increasing numbers as the weather grew warmer, until a peak was reached in the latter part of July, when as many as 200 flies were caught in one hour, in an area of one acre. The volant population then seemed to diminish during August and September. A fair number were seen on warm days in October and November, and 4 flies were flying as late as December 8. These swarms of volants rapidly build up the summer population of the deälated keds on the deer. The fluctuations of the ked populations of *Neolipoptena ferrisi* and *Lipoptena cervi* presumably follow the same pattern. It is known for both these species that some of the adults remain on the host throughout the winter. Cameron (1932, p. 87) found *L. cervi* most abundant on red deer, *Cervus elaphus,* in Scotland, from July to October.

Lynchia americana is a common Nearctic parasite of a variety of unrelated hosts, as shown later in this section and in Part II. In spite of its abundance in the United States, it is practically unknown from Mexico and farther south. There is conclusive evidence that the adults live the year round on certain resident birds, even in the most northern areas, and may occur during the winter in large numbers and go on breeding on such hosts. Owls seem to be favorite winter hosts. Champlain (1947) states that the fly is common in Pennsylvania on the great horned owl, *Bubo v. virginianus,* from November until March, at which season he also took puparia from the feathers. Mr. Roy Latham sent me 14 flies from a great horned owl, caught at Orient, New York, January 1, noting that ''a bird of this species has plenty of heat and is heavily feathered, so that the flies would have ample shelter while concealed in the plumage.'' Some other winter dates of *L. americana* from great horned owls are as follows: in Ontario, December 1 (10 females on one bird; Judd, 1951); Massachusetts, December 2, 24 and 31; New York, September 21 and January 20; Ohio, October 15; Michigan, one gravid female, December 14; Tennessee, December 24; Maryland, November 19 and March; and Mississippi, January 20. From other owls there are recorded captures in New Hampshire, April 9, Massachusetts, November 1, and Ontario, November 4. The ruffed grouse, *Bonasa umbellus,* is also a frequent winter host: in New Hampshire, November 6; Pennsylvania, March 4; and New York, October 23. I have also seen specimens taken on red-tailed hawk, *Buteo jamaicensis borealis,* in New Jersey, October 10, and in New York, November 27 and December 16. It occurred on a marsh hawk, *Circus cyaneus hudsonius,* in Massachusetts, February 18.

Lynchia fusca, common on owls in the western and southern United States, *Lynchia hirsuta,* of quail, and *Stilbometopa impressa,* also of quail, possibly follow the pattern of *L. americana* and hibernate as adults on the hosts. I have seen several *L. fusca* taken from owls at Sacramento, California, March 11 and 19, and others from an owl burrow at Tracy, California, April 26. Mrs. Laskey

(1941) reports a specimen from a saw-whet owl, *Aegolius acadicus,* in Tennessee, on March 16; specimens were taken in Mississippi on a barred owl, *Strix varia,* January 24, and on a screech owl, *Otus asio,* March 11. A gravid female of *S. impressa* was found on a quail at Bakersfield, California, in November.

The observations summarized in a previous section on larviposition show that *Crataerina pallida, C. melbae, Stenepteryx hirundinis,* and *Ornithomyia biloba,* of the Old World swallows and swifts, hibernate as puparia in or near the deserted nests of their hosts. The section on the duration of pupal development discussed also the so-called ''summer'' and ''winter'' puparia produced by these and possibly by other Hippoboscidae. Nevertheless, it remains questionable whether or not and to what extent adults of these flies are in addition carried by the birds to the hosts' winter quarters, and whether any adult flies ever travel north with the spring migrants. These problems are complicated at present by the unsatisfactory taxonomy of *Crataerina* and *Ornithomyia.* It should be determined first which of the species now regarded as specific parasites of the Paleotropical swifts and swallows are actually distinct from *C. pallida* and *O. biloba.*

Much has been published on the common Holarctic species of *Ornithomyia,* which probably have been more intensively collected than any of the other hippoboscids. Unfortunately the older information is of little value, because the species were not properly understood until some 20 years ago; even now there is some disagreement about the status of one of the forms. The following discussion recognizes two species only: *O. avicularia,* a strictly Old World fly, and *O. fringillina,* of both the Nearctic and Palearctic Regions; *O. lagopodis* is here considered a synonym of *O. fringillina.* It should be pointed out particularly that until recently all the so-called *O. avicularia* of American writers were *fringillina;* I have never seen a specimen of true *O. avicularia* from the New World. Prior to 1936, when Thompson published some notes on one of Curtis' types of *O. fringillina,* the *O. avicularia* of most European writers (Bezzi, 1905; Austen, 1906; Massonat, 1909; Falcoz, 1927; etc.) was a mixture of true *O. avicularia* and *O. fringillina,* sometimes even including *O. biloba.* On the other hand, Bezzi (1905) and other European continental writers often applied the name *O. fringillina* to *O. biloba,* a parasite of the barn swallow, *Hirundo rustica;* as this fly is unknown from the British Isles, it could not possibly have been Curtis' species. I am using here only data definitely referable to either *O. avicularia* or *O. fringillina.* Enough of these are available to show that, although structurally very close, these two species differ markedly in their distribution and ecology.

O. avicularia is very widely distributed in the Old World, being by no means confined to the Palearctic Region. It is definitely known from England, Wales, Ireland, southern Norway and Sweden, central and southern Russia, Poland, Germany, Bavaria, Denmark, the Netherlands, Belgium, France, Switzerland, Austria, Albania, Bulgaria, Italy, Spain, Portugal, the Canary Islands, Cyprus, Egypt (Red Sea), Belgian Congo, Tanganyika, Ceylon, Tonkin, Australia, Tasmania, New Zealand and New Caledonia. I have seen specimens from most of these areas. *Ornithomyia nigricornis* Erichson (1842), *O. opposita* Walker (1849), and *O. tasmanensis* Macquart (1851), described from the Australian Region, appear to be indistinguishable from Palearctic specimens of *avicularia.* I suspect that eventually *O. avicularia* will be recognized as one of the common hippoboscids of the Paleotropical Zone, where very little collecting of bird parasites has been done as yet. In Europe it does not extend as far north as *O. fringillina.* It is very rare in Scotland (Thompson, 1940, p. 114), though not entirely lacking, as shown by specimens taken at Dunalastair, Perth, on the jay, *Garrulus glandarius rufitergum,* and the song-thrush, *Turdus e. ericetorum,* by R. Meinertzhagen. This contrasts with some 70 lots of *O. avicularia* seen from England and Wales. In addition to a very wide geographical range, *O. avicularia* also has an unusual variety of hosts. Even if restricted to birds from which I have seen it myself, the list now comprises some 52 species in the Palearctic Region alone and some 20 additional resident birds elsewhere; it will no doubt be greatly extended in the future. A sizeable proportion of these birds act as effective breeding hosts. Most of the Palearctic host species are also infested with *O. fringillina,* so that the two flies possibly compete for the same birds where their territories overlap, a matter which was briefly considered before.

The occurrence in both the Temperate and Tropical Zones and the wide host range conspire to make the seasonal fluctuations of *O. avicularia* extremely complex and a problem well worthy of a special inquiry; but the information now at hand is inadequate for the purpose. We need above all to be better informed about the relative abundance of the insect and the exact nature of its host-parasite relation in the tropics. Presumably in the Mediterranean Subregion, tropical Africa and Asia, and the warmer sections of Australia, it breeds without interruption the year round and its population remains fairly constant on the local resident hosts.

What influence has this on the fly population of temporary winter immigrants from colder temperate areas? Do the tropical and subtropical flies serve to some extent as a reservoir from which the migratory birds might draw a supply carried back in spring to the colder breeding areas, where such imported flies might help build up the summer population? It is fairly certain that in northwestern Europe the adults of *O. avicularia* disappear from the resident bird population during the winter. There is also some evidence that the fly survives there as puparia in or near the nests. In Denmark the adults occur on birds from July 1st to November 30 (Johnsen, 1948, p. 287), being particularly common in July. In southern England the adult season is more extended, lasting from April to November (April 16 to November 14, according to Thompson, 1937; June 4 to November 16, according to Ash, 1950). Ash (1951) furnished the only definite information on the occurrence of *O. avicularia* on migrating birds in the fall. Between August 27 and September 15, 1950, he examined in Oeland, southern Sweden, 1482 trapped birds of 56 species. Only 34 of these, of 15 species, carried either *O. avicularia* or *O. fringillina,* except for one mixed infestation. Of a total of 41 flies collected, 19 were *O. avicularia,* from 12 birds of 5 species. The very low rate of infestation suggested to Ash that the majority of the flies leave the host prior to migration; to support this surmise he cited the fact that, with one exception, all the flies taken were females, most of them gravid. It is more likely, however, that the adults perish at the normal rate on the migrating hosts, but can no longer be replaced by newly-emerged flies, while the females normally live longer than the males. It would be most interesting to know the fate of the surviving flies during the southward journey and in the winter quarters. Possibly they help build up the general fly population in the southern areas; that any of them ever survive the winter and return north with the host is most improbable, in view of the short lifetime of the adult Hippoboscidae. In the section on the larviposition I reviewed the few records of puparia collected in the winter in Germany, England, the Netherlands, Belgium and Denmark.

In the Old World, *O. fringillina* is a strictly Palearctic fly, which extends much farther north than *O. avicularia* and avoids the tropical areas entirely. It is definitely known from Iceland, the whole of the British Isles (including Scotland and the Shetlands), the whole of Scandinavia (including Lapland), Finland, the whole of Russia, Esthonia, Germany, Denmark, the Netherlands, Belgium, France, Switzerland, Austria, northern Italy, Siberia, Manchuria, China (Fukien and Shantung Provinces), and Japan. It is common in the summer in northern Europe. I have seen some 30 lots from Scotland and the Shetlands, in contrast to the 2 Scottish lots of *O. avicularia.* It is also the hippoboscid with the World's northernmost record (near 70° N. in Finland). The ability to thrive in the summer in the subarctic parts of Eurasia no doubt explains how it was able eventually to reach North America, either across the Straits of Behring or by way of the Aleutian Islands. *O. avicularia* failed to do this owing to its more southern distribution. In the New World, *O. fringillina* is essentially a Nearctic insect, which practically stops at the northern Mexican border. There are only 2 records from the high plateaux of Mexico, where the fauna comprises several other Nearctic elements. Again *O. fringillina* extends farthest north of any American hippoboscid (68° N. in Alaska), though not nearly as far as in Europe.

The list of the known hosts of *O. fringillina,* discussed later in detail, is even larger than that of *O. avicularia.* In the Palearctic Region it comprises at least 73 species and in North America some 104 (4 common to both continents). *O. fringillina* differs markedly from *O. avicularia* in that it includes among its breeding hosts a fair number of permanent residents, on which part of the adult population might conceivably survive the winter and possibly even continue to breed, at least in the warmer temperate areas. Since adults are practically unknown from the tropical and subtropical winter quarters of some of the migratory hosts, many adult *O. fringillina* must die before the birds start migrating or shortly afterward. The evidence that *O. fringillina* overwinters in Europe mainly or perhaps exclusively as puparia is somewhat more complete than for *O. avicularia,* as may be seen from my account of the larviposition. In Denmark, the adults were taken on birds from July 20 to November 13 (Johnsen, 1948, p. 290); but the latest occurrence was on a migrant. In England the flies have been observed on birds from early in April to November (June 18 to October 16, according to Thompson, 1937, 1938; April 6 to September 9, according to Ash, 1950). They are most abundant during July, August and September, after which the proportion of infested birds decreases rapidly. Few flies occur on migrants in the fall, as shown by Ash's (1951) observations in southern Sweden. Of 1482 birds of 56 species trapped between August 27 and September 15, 1950, only 22 of 13 species carried *O. fringillina,* one fly in each case. Similar observations were made on this species in North America, where adults have been taken from April to November (latest capture on record on November 12 in Oregon). Johnson (1929, p. 51), referring to the New England flies, stated that *O. fringillina* "is confined to the strictly migratory species (its occurrence on other birds being accidental); that they must be on these birds on their return in the spring; that the fly probably reproduces only in the summer and early autumn, usually depositing its pupa in the nest of its host. The fly on emerging from the pupae naturally seeks the fledglings and is slow in deserting a young for an adult bird. The parent flies which were on the adult birds probably die after depositing at most two pupae." These conclusions agree on the whole with the facts as known at present and particularly with the failure to find thus far puparia of *O. fringillina* during the winter in the northern United States, although this may be due to incomplete observations. If they are correct, it must be assumed that the fly continues to reproduce in winter on both migratory and resident birds in the southern states, especially in those bordering the Gulf of Mexico. Many of the regular breeding hosts of the fly are known to winter there. Positive information on the proportion of migrants infested with the fly on the northward return journey in the spring would be most desirable. According to Johnson (1929, p. 51), F. A. Saunders searched carefully for parasites on some 400 purple finches, *Carpodacus purpureus,* 88 tree sparrows, *Spizella arborea,* and 68 other birds, trapped for banding at South Hadley, Massachusetts, between February 8 and May 14, without finding a hippoboscid. The earliest recorded capture in Massachusetts is on July 3 from a song-sparrow, *Melospiza melodia.*

Wülker (1925*b*, p. 226) and Eichler (1939, p. 219) attempted to link the yearly cycle of the hippoboscids of Central Europe with that of the hosts. The common bird-flies of that area, *Ornithomyia avicularia, O. fringillina, O. biloba, Crataerina pallida,* and *Stenepteryx hirundinis,* infest mostly Passeriformes which raise regularly two broods of young during one summer. It is assumed that the flies parasitize mainly nestlings and juvenile birds and have likewise only two generations a year. The flies emerging from overwintered puparia feed on the first brood of birds and their parents, producing puparia from which the second fly generation emerges. This second generation feeds on the second brood of birds and the parents, and deposits puparia which hibernate as such and which the following spring produce next year's first generation. The parallelism between the rearing of the young by the avian hosts and the parasites' reproductive cycle is supposedly due to both the juvenile birds and the majority of the flies being bound to the nests. Since there is no such link between the young and the nest among the mammals, there is no similar connection between the reproductive cycle of the mammalian hippoboscids and that of their hosts. These different types of hippoboscid cycles were contrasted by Eichler in two diagrams.

Original and Acquired Breeding Hosts. It might be useful to attempt a distinction between original and acquired breeding hosts, particularly for the later discussion of the origin of the Hippoboscidae of domesticated animals. Hopkins' (1949, p. 426) terminology of ''primary'' and ''secondary'' infestations corresponds on the whole to my terms ''original'' and ''acquired.'' I am reluctant to adopt them because the author ties them up with the phylogeny of the hosts. While this point of view may be justified in the case of lice, it is of doubtful value for the Hippoboscidae, as will be shown later.

There is some slight evidence that a species of louse-fly may sometimes acquire a new satisfactory breeding host by accidental straggling under natural conditions. That this is by no means easy is well shown by the New World history of the common pigeon-fly, *Pseudolynchia canariensis.* Originally this fly was restricted to the Old World, particularly the tropical and subtropical parts of Africa and southern Asia, where it now breeds in nature on several species of wild pigeons (Columbidae), including the rock dove, *Columba livia,* the wild ancestor of the domestic bird, and possibly on some other types of birds. It was brought to America by Man with domestic pigeons, probably at a comparatively recent date (first published record in 1885), and has been extending its range gradually in the United States during the past 50 years. Although it is at present often abundant from the central United States to the northern half of Argentina, there is no reliable evidence that it has strayed thus far to any of the wild American Columbidae or to any other native host. Statements to the contrary have always proved erroneous when properly investigated. For instance, Beatty (1947, p. 154), listed it (as *P. maura*) from the Virgin Islands ground dove, *Columbigallina passerina nigrirostris,* in St. Croix; his specimens proved to be *Microlynchia pusilla,* the native American pigeon-fly, although I found them placed in the U. S. National Museum with *P. canariensis.* I suspect, nevertheless, that in due time *P. canariensis* will become established in nature on one of the wild American Columbidae. Coatney (1931; 1933) maintained it in the laboratory for 44 days on the North American mourning dove, *Zenaidura macroura carolinensis,* during which time it voided normal puparia which later produced adults. Kartman (1949, pp. 128–129), in Hawaii, also kept it alive for several days in captivity on a Chinese spotted dove, *Streptopelia c. chinensis,* and on a ringneck dove, *Streptopelia d. decaocto;* but he noted that these doves did not acquire the fly in the zoological park where they were housed in the vicinity of infested domestic pigeon lofts.

Kartman (1949, p. 131) attempted to maintain *Olfersia aenescens*, a specific parasite of oceanic birds, on domestic pigeons in Hawaii. Most flies were apparently not interested in the strange host. Of 20 flies removed from a red-footed booby, *Sula sula rubripes*, and placed in a cage with a pigeon, only one was recovered alive 10 days later and showed fresh blood in the mid-gut. Two other flies, bred from puparia, remained on a pigeon from April 24 to May 4.

The New World *Microlynchia pusilla*, a parasite of native American pigeons, seems to be more adaptable to new hosts than *Pseudolynchia canariensis*, since it is now taken occasionally on domestic pigeons, even on young squabs. On one occasion, it was found also on an introduced Chinese spotted dove, *Streptopelia c. chinensis*, a bird now feral in southern California. There is no positive evidence as yet, however, that *M. pusilla* uses either of these new hosts for breeding purposes, though it may be expected to do so eventually. The American *Stilbometopa podopostyla* also seems to attempt becoming established on domestic pigeons, on which it has been taken several times in the United States and in Colombia. The common North American *Ornithomyia fringillina* likewise occurs occasionally on the introduced English sparrow, *Passer domesticus*, and starling, *Sturnus vulgaris;* but this is to be expected, since both birds are among the known hosts of *O. fringillina* in the Old World. *Ornithoica vicina* also tends decidedly to become established on the introduced English sparrow, *Passer domesticus,* both in the United States (5 records to date from Maine, the District of Columbia, Maryland, Kansas, and California) and in Hawaii.

Two other common American flies, *Lynchia americana* and *Ornithoctona erythrocephala*, became established on the pheasant shortly after this game bird was brought by Man from Europe. These seem to be true cases of spontaneous acquisition of new breeding hosts; they are not too surprising in view of the very loose specificity of the flies. *L. americana* has at least 15 native breeding hosts, including the native grouse, *Bonasa umbellus*, and quail, *Colinus virginianus*. *O. erythrocephala* has 9 breeding hosts in North America alone and many more in South America.

In the northeastern United States, the European deer-ked, *Lipoptena cervi*, is another example of a fly acquiring new breeding hosts under natural conditions. This parasite was, in my opinion, brought from the Old World by Man with European deer. From this host it strayed to the native Virginia deer, *Odocoileus virginianus*, on which it now breeds at several localities in the northeastern United States. It has also been reported from the native wapiti, *Cervus canadensis*; but whether this animal is a breeding host is uncertain. The exact date of the introduction is unknown; it was first recognized in the United States in 1907, when it was described as a new species by Coquillett (*L. subulata*). If it were truly native, or autochthonous, it would be found over a much wider territory and be more abundant; while its presence on native deer could scarcely have escaped the early American entomologists.

Fly Specificity and Host Relationship. In view of the emphasis placed by some recent writers on a possible parallel evolution of certain ectoparasites and their vertebrate hosts, it may be useful to analyze the occurrence of hippoboscids in the major groups, or lines of descent, of mammals and birds. Orders and families would seem to be most suitable for the purpose, being neither too broad nor too narrow; although it should be kept in mind that most so-called ''orders'' of birds have not the phylogenetic or morphological value of the accepted orders of mammals, being clearly of a lower rank (perhaps corresponding mainly to ''families'' in mammals). As will appear from the following discussion, hippoboscids are associated *for breeding purposes* with few living orders of mammals (5 out of 18) and many more orders of birds (18 out of 27). It should not be inferred from this that adaptive radiation was necessarily more active among the louse-flies of birds. On the contrary, the relatively few species of flies found on mammals are sharply differentiated into four lines of descent (subfamilies Hippoboscinae, Melophaginae, Ortholfersiinae and Alloboscinae); whereas the more numerous flies of birds form only two such lines (subfamilies Ornithoicinae and Ornithomyiinae).

I have attempted to determine, in so far as warranted by the information now available, the true breeding hosts of the several species of flies, that is, the hosts on which they are able to reproduce continuously under natural conditions, and I have distinguished these from stray or accidental occurrences. Of course, this can be done only for the more commonly collected flies, where numerous records, from many localities and several sources, allow fairly reliable conclusions. Most of the louse-flies of mammals are in this case; whereas the data are as yet unsatisfactory for nearly half of the known bird-flies. The ecological aspect of the host-parasite relation is also stressed. It is not merely interesting in itself; in my opinion it is of prime importance in determining the fly's choice of a given host for breeding purposes.

Within each order the known hosts are discussed by families and are traced, as a rule, to the genera. Host species are mentioned only when important for some special reason. The majority of records cited are based on my own identifications, those from the New World being listed later in detail in Part II of the present work. Published host records which I was unable to verify are mentioned only when they seem fully reliable; if some of those given by other authors are not included, it does not mean that I am unacquainted with them. Specifically, many published European host records of *Ornithomyia avicularia* and *O. fringillina* must be disregarded, since until recently these two species were generally confused, not only with each other but also with *O. biloba.*

I. Birds. I have adopted the names and sequence of the orders in J. L. Peters' "Check-List of Birds of the World" (1931-1951). The limits and names of the families are those of the "Classification of Recent Birds," by E. Mayr and D. Amadon (1951), from which I have taken also the number of species which follows each family name in parentheses. A. Wetmore's (1951) "Revised Classification" differs only in minor details, and is not as useful for my purpose.

No true breeding hosts of louse-flies are known from the following orders: Rheiformes, Casuariiformes, Apterygiformes, Sphenisciformes, Gaviiformes, Podicipiformes, Anseriformes, Coliiformes and Piciformes. Some of these are mentioned below because of stray occurrences.

The few reports of strictly mammal-infesting flies straying to birds should be mentioned. They are mostly species of *Hippobosca,* in the Old World: *H. equina* (of equines and cattle) and *H. longipennis* (of dogs and other Carnivora), to be discussed later in detail; and *H. fulva* (of antelopes) on the purple-crested lourie, *Gallirex porphyreolophus porphyreolophus.* The North American *Neolipoptena ferrisi* (of deer) is reported from the sharp-shinned hawk, *Accipiter striatus velox,* Pacific horned owl, *Bubo virginianus pacificus,* and California valley quail, *Lophortyx californica californica.* The belief that the volants of the European deer-ked, *Lipoptena* *cervi*, first live for a time on game birds in the fall, retaining their wings meanwhile, and later move to deer, has no basis in fact, as I ascertained before (J. Bequaert, 1942*a*, p. 75).[18] Johnsen's (1948, p. 282) report of a volant *L. cervi* from a peregrine, *Falco peregrinus*, in Bornholm, Denmark, in September, seems to be the first from a bird that is fully reliable. Possibly some of the captures of *Hippobosca* and *Neolipoptena* from birds, mentioned above, are also unreliable. In any case, there is no certainty and little likelihood that any of these flies did bite the birds on which they were found.

1. Order Struthioniformes (Struthiones). One family, the Struthionidae, with 1 species, the ostrich, *Struthio camelus*, nowadays restricted to Africa. It harbors a specific louse-fly, *Hippobosca struthionis*, known thus far only from Kenya, Tanganyika, Transvaal, Cape Province, Bechuanaland and South-West Africa; not from the more northern part of the host's range. There are a few stray records from the horse and dog in Kenya (Bequaert, 1939*b*, p. 88); Dr. H. Oldroyd sent me a specimen that had strayed to a Grant's gazelle, *Gazella granti*, in Kenya. The fly is of unusual interest, as the other 7 species of the genus breed only on mammals. Moreover, *Hippobosca* is the only hippoboscid genus occurring normally on birds and mammals, though the same species never breeds on both types of hosts. The 8 known species are all closely related and apparently on the same evolutionary level, so that it is difficult to decide whether the ostrich-fly is a relict of a primitive bird-inhabiting hippoboscine stock or was derived later from a mammal-infesting ancestor; though I am inclined to adopt the latter view. Ostriches are very large, flightless, cursorial birds, having ecologically little in common with most of their present-day avian relatives and behaving more like certain African ruminants and equines, with which they are sometimes associated in mixed herds. It is interesting to note in this connection that intestinal nematodes of the group of the sclerostomes, otherwise represented by several species in the African wild equines, occur also in the African ostrich and in the South American rhea, alone among birds. The ostrich and rhea also share the same parasitic mite, *Eupterolichus bicaudatus* (Gervais), not known from any other host. No hippoboscid is known from the rhea.

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[18] The attractive tale of *L. cervi* using the European capercaillie ("Auerhuhn"), *Tetrao urogallus*, as a temporary host in the fall was recently revived by Eichler (1952, p. 232), however not from actual observation. Thus far I have not met with a trustworthy record of such an occurrence. Hunters' reports are not to be trusted, unless the specimen is captured and named by a competent dipterist. They are probably all based on failing to recognize *Ornithomyia fringillina*, which is known to occur on the capercaillie or related game birds in Europe and North America.

2. **Order Tinamiformes (Crypturi).** This contains the relatively small, strictly Neotropical family Tinamidae (33), or tinamous. The single record of *Olfersia coriacea* (= *P. meleagridis*) from *Tinamus solitarius*, in Brazil, by Lutz, Neiva and da Costa Lima (1915), was believed by these authors to be accidental; but I am inclined to discard it as a contamination. However, species of *Crypturellus* are infested fairly often with *Microlynchia pusilla* and *M. crypturelli*, which seem to use these birds for normal breeding, even though they are known from other hosts also. It is possible that tinamous may be regular breeding hosts of *Stilbometopa podopostyla*, since 4 of the 11 known wild hosts of this fly are species of *Tinamus* and *Crypturellus*. The few records of *Ornithoica vicina* on *Crypturellus* are more probably accidental. The one reported occurrence of *Lynchia holoptera* on *Rhynchotus* was probably based on a stray or error, the fly being otherwise specific of rails (Gruiformes).

3. **Order Gaviiformes (Gaviae).** One family, the Gaviidae, or loons, with a single, northern, circumpolar genus, *Gavia* (4). The one record of *Olfersia fumipennis* on *Gavia immer*, in Wisconsin (Johnson, 1922), was evidently a stray, the fly being otherwise a specific parasite of the osprey, *Pandion haliaetus*.

4. **Order Podicipiformes (Podicipedes or Colymbiformes).** The Podicipidae (20; Colymbidae of Peters), or grebes, marine birds of the Northern Hemisphere, are not known as breeding hosts of louse-flies. I can find only one published record of *Ornithoica confluenta* (= *O. podicipis*) from an undetermined African grebe (*Podiceps* = "*Colymbus*") ; but it is highly dubious and may have been due to some contamination or error.

5. **Order Procellariiformes (Tubinares).** Marine, fish-eating birds, cosmopolitan, but mostly of tropical and southern seas, breeding in colonies on small, rocky oceanic islands, without building true nests. No flies are known from the Pelecanoididae (4).

In the Diomedeidae (13), Coquillett (1904) reported 4 specimens of *Olfersia aenescens* (= *Pseudolfersia diomedeae*) from a Galapagos albatross, *Diomedea irrorata*, and this host was later confirmed by F. X. Williams.

The Procellariidae (73) have a few records of *Olfersia aenescens* from shearwaters (*Puffinus*) and petrels (*Pterodroma*), in Oceania (Bequaert, 1941*b*, p. 227). Normally this fly is more a parasite of Pelecaniformes (boobies, *Sula*) and it is also reported from Charadriiformes (noddies, *Anous;* sooty terns, *Sterna*). Possibly Procellariiformes are never more than occasional hosts of *O. aenescens*, which strays to them at nesting sites also occupied by other, true breeding hosts.

6. **Order Pelecaniformes (Steganopodes).** This order comprises 5 families of so-called swimmers, marine or aquatic, mainly fish-eating birds, which usually breed in colonies or rookeries without building much of a nest. The birds and particularly their nestlings are frequently infested with flies, which at times swarm over the breeding sites. As some of the hosts are nearly cosmopolitan, at least in tropical seas, their flies also are widely distributed.

In the Phaëthontidae (3), *Olfersia aenescens* occurs commonly on tropic birds (*Phaëthon*) in Oceania. Dr. James P. Chapin informs me that on Ducie Island adult *Phaëthon rubricauda* were infested with from 12 to 18 flies per bird; the dark-colored flies showed up as dusky spots just under the fringes of the feathers on the fore-neck and breast as the birds sat on the nests (Fig. 21).

The Fregatidae (5), or man-of-war birds (*Fregata*), all share *Olfersia spinifera.* This fly has been reported occasionally in print from other hosts and I have seen specimens labelled as taken from the pelican and cormorant; I am now inclined to regard all such records as strays, if not errors or *post mortem* contaminations. The association of *O. spinifera* with *Fregata* is one of the most pronounced cases of host specificity known in the Hippoboscidae. It is particularly remarkable that the closely allied and widespread *O. aenescens* avoids man-of-war birds altogether.

In the Phalacrocoracidae (31; including Peters' Anhingidae), the American cormorants (*Phalacrocorax*) are regular breeding hosts of *Olfersia fossulata* and sometimes of *Olfersia sordida;* while the African species (*Phalacrocorax* and *Haliëtor*) frequently harbor *Lynchia schoutedeni*, which is almost specific of these birds. The snake bird, *Anhinga anhinga*, is also a host of *Lynchia schoutedeni* in Africa (on the race *A. anhinga rufa*).

In the Sulidae (9), both *O. aenescens* and *O. fossulata* are usual parasites of boobies (*Sula*), which they use as breeding hosts.

In the Pelecanidae (6), pelicans (*Pelecanus*) appear to be regular breeding hosts of *O. fossulata* and even more often of *O. sordida.*

It is of some interest that of the 7 known species of *Olfersia*, 4

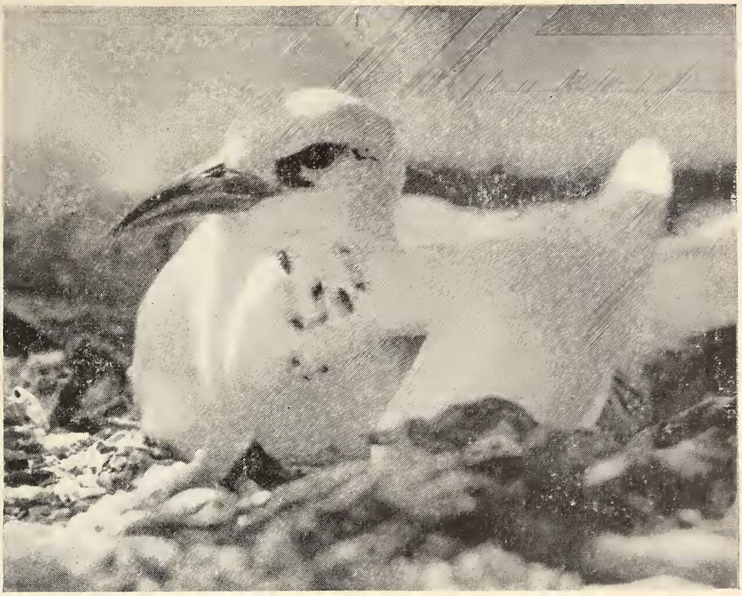

FIG. 21. Red-tailed tropic bird, *Phaëthon rubricauda* Boddaert, carrying *Olfersia aenescens* Thomson. Ducie Island. Photograph by Dr. J. P. Chapin, January 3, 1935. (By courtesy and with permission of American Museum of Natural History).

have become closely associated with Pelecaniformes, although perhaps only one (*O. spinifera*) is strictly specific for the order.

7. **Order Ciconiiformes (Gressores).** The wading birds or waders comprise 4 families, of which one, the Scopidae (1), or hammerheads of Africa, is not known to harbor flies. They are mostly aquatic, mainly fish-eating, and construct loose, untidy nests, often in a damp environment; but the nests themselves are usually raised above the ground, not in wet situations. Many waders are large, densely clothed in long plumage, with a long heavy bill seemingly ill-suited to destroying ectoparasites. While the birds themselves thus offer excellent shelter for adult flies, their aquatic habits and perhaps their nesting behavior render fly reproduction hazardous. This may explain why the hippoboscids of waders, although by no means rare, belong to a few species which may have developed some special means, as yet unknown, of protecting the puparia in the peculiar habitat of the hosts. Unfortunately the larviposition of the specific louse-flies of waders has not been observed.

The few species regularly breeding on waders belong to the genera *Ornithoica* and *Lynchia.* They occur on Ardeidae (59. Cosmopolitan; including Peters' Cochleariidae), Threskiornithidae (28. Cosmopolitan), and Ciconiidae (17. Cosmopolitan), being either restricted to them or occurring also on some of the ecologically similar Gruiformes and Charadriiformes. They show little further selectivity within the order itself and are sometimes nearly cosmopolitan. Thus *Lynchia albipennis* (= *L. ardeae*) is a world-wide specific parasite of Ardeidae (*Ardea, Butorides, Egretta, Florida, Bubulcus, Nycticorax, Ardeola, Ixobrychus, Botaurus, Leucophoyx, Casmerodius, Nyctanassa, Hydranassa, Dichromanassa, Tigrisoma,* and *Cochlearius*), Threskiornithidae (*Mesembrinibis, Guara,* and *Theresticus*), and Ciconiidae (*Mycteria* and *Ibis*); but it has also been taken, presumably as a stray on Gruiformes (*Gallinula, Porzana, Porphyrula,* and *Eurypyga*) and Charadriiformes (*Actophilornis, Tringa,* and *Xiphidiopterus*), as well as exceptionally on gulls, owls and diurnal birds of prey. *Ornithoica confluenta* (=*O. beccariina*)[19] may have similar host preferences and distribution, but has as yet been too little collected. Thus far it is definitely known from Ardeidae only (*Casmerodius, Bubulcus, Leucophoyx, Ixobrychus,* and *Butorides*). The one record from a grebe (*Podiceps*), in Africa, is either unreliable or based on a stray, as noted under Podicipiformes.

In addition, wading birds may harbor as strays other common bird-flies. There are several records of *Ornithomyia avicularia* from *Ardea, Nycticorax,* and *Botaurus,* in Europe. *O. fringillina* was taken on *Ciconia* in Europe; and Massonat (1909) records *Ornitheza metallica* from *Ardea cinerea* in France. *Lynchia americana* was found on *Casmerodius* in North America; *L. schoutedeni* also on *Casmerodius* in China; *Ornithoctona erythrocephala* on *Butorides, Leucophoyx,* and *Nyctanassa* in the Antilles, on *Nycticorax* in Brazil, and on *Botaurus* in Canada; *Ornithoctona plicata* and *Ornithoica pusilla* on *Demigretta* in the Pacific Islands; and *O. pusilla* on *Lophotibis* in Madagascar. I have seen a *Pseudolynchia canariensis* labelled as taken on *Hagedashia* in Uganda.

Finally, mention should be made of *Lynchia massonati* Falcoz

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[19] It should be noted that the fly usually called *Ornithoica confluenta* by American writers is not Say's *confluenta,* in my opinion, but a distinct species, *Ornithoica vicina* (Walker). The true *O. confluenta* breeds on waders only, whereas *O. vicina* breeds on other types of birds.

(= *L. americana* Massonat, 1909; not of Leach), based on a fly taken in France on a spoonbill, *Platalea leucorodia* (Fam. Threskiornithidae). Its correct identity must, however, be left in abeyance, although it is most probably identical with some other described species (? *Lynchia schoutedeni*).

The Phoenicopteri or flamingos, family Phoenicopteridae (6. Cosmopolitan), are united with the Ciconiiformes by Peters, while Mayr and Amadon regard them as a distinct order. They do not act as breeding hosts for any known fly; but I have seen a specimen of the common African *Ornithoctona laticornis* (= *platycera*) said to be from *Phoeniconaias minor* in Kenya, either a stray or a contamination.

8. **Order Anseriformes (Anseres).** The large group of the waterfowl, with the two families Anatidae (145. Cosmopolitan) and Anhimidae (3. South American), comprises aquatic birds with dense, but rather short and oily plumage, which nest in very damp situations, the young usually leaving the nest immediately after hatching. These features no doubt explain why they do not serve as breeding hosts to any known hippoboscid. The following records may safely be disregarded as either strays or contaminations, without further significance. One *Ornithoctona erythrocephala* is labelled from a Canadian goose, *Branta c. canadensis*, in North Carolina; one *Lynchia albipennis* from a duck, *Anas brasiliensis*, in southern Brazil; and one *Ornithoctona laticornis* (= *platycera*) from a knob-billed goose, *Sarkidiornis melanotos*, in Central Africa.

9. **Order Falconiformes (Accipitres).** Most diurnal birds of prey are fairly large to very large, covered with long soft, closely appressed contour feathers, and provided with a broad, hooked bill. They feed mainly on other birds or on mammals, usually caught alive, more rarely on fish, mollusks, insects, carrion, or even vegetable matter. All are powerful fliers, often covering considerable territory and some migrating at regular seasons. The nests are fairly durable, though loosely constructed, and placed in dry locations, usually above the ground, often in trees or in lofty aeries. Together with the Strigiformes and Passeriformes, they are among the most favored hippoboscid hosts. The dense plumage offers ideal shelter for the flies, while the bird's clumsy, hooked bill is ill-adapted to catching ectoparasites. These features, also present in the Strigiformes, may explain to some extent why both diurnal and nocturnal birds of prey sometimes show unusually heavy individual infestations with flies.

No flies have been recorded thus far from the Sagittariidae (1.

African), the secretary bird, *Sagittarius serpentarius*, which, moreover, does perhaps not properly belong in this order.

Of the remaining four families, two each have a highly specific louse-fly. The Cathartidae (6), or American vultures, are the only true breeding hosts of *Olfersia bisulcata*, known at present from four of the five genera of the family (*Vultur*, *Sarcoramphus*, *Coragyps*, and *Cathartes*); there is no reliable record of this fly from any other type of bird. *Olfersia fumipennis* breeds only on the Pandionidae (1), or the osprey, *Pandion haliaetus*, throughout most of the nearly world-wide range of this bird; the one or two records from other hosts, if at all trustworthy, are certainly accidental. It may be of some significance that the genus *Olfersia*, one of the most distinct in the subfamily Ornithomyiinae, does not use other Falconiformes as breeding hosts, though sometimes straying to them. Some ornithologists have suggested that the Pandionidae, and even more so the Cathartidae, are not or only remotely related to the Falconidae and Accipitridae. Furthermore, it is remarkable that the two American species of *Lynchia* commonly found on Accipitridae and Falconidae, discussed below, seem to avoid the Cathartidae and Pandionidae. I know of only one record of *L. angustifrons* and two records of *L. nigra* from *Cathartes*. Other Hippoboscidae also stray very rarely to vultures and the osprey. There are a few records of *Lynchia albipennis*, *Ornithoctona erythrocephala*, and *Ornithomyia fringillina* from *Pandion* in North America. An unusual case is that of a western turkey vulture (*Cathartes aura teter*) in Oregon, carrying an *Ornithomyia fringillina* with 4 Mallophaga attached; the lice were a species of *Brüelia* of a type normally found only on passerines, proving that the fly had recently reached the vulture from a bird caught as prey.

The Hippoboscidae found on the Falconidae (58. Cosmopolitan) and Accipitridae (205. Cosmopolitan), the falcons, hawks, eagles and their allies, show no very strict specificity. They are perhaps better known than the flies of other birds, due to their frequent abundance on individual birds and the large size of the hosts, which are, moreover, thoroughly hunted and seldom protected. The unusually large number of reliable records fall into three groups, according to the decreasing degree of specificity. None of the flies are as narrowly specific as the two species of *Olfersia* of the vultures and the osprey mentioned above.

(1) Several species are specific breeding parasites of diurnal birds of prey, but show little or no further preference for either the Falconidae or the Accipitridae, nor for any of the genera.

Flies of this type probably occur in all parts of the Globe, except in the Palearctic Region. The New World, where they are best known, has three such species. The small *Lynchia angustifrons* is common on *Accipiter, Buteo, Busarellus, Elanus, Odontriorchis, Leucopternis, Micrastur, Falco, Milvago, Hypomorphnus,* and *Ictinia;* it has been taken exceptionally on a vulture (*Cathartes*), but its sporadic occurrence on other types of birds is due to straggling. The larger *Lynchia nigra* shows similar host preferences, being known from *Accipiter, Aquila, Buteo, Buteogallus, Circus, Falco, Geranospiza, Herpetotheres, Heterospizias, Leucopternis, Milvago,* and *Polyborus;* there are also some records from vultures (*Cathartes*) and strays from a cuckoo and an owl. A comparison of the two lists suggests that each fly possibly chooses a slightly different type of diurnal bird of prey, since there is little duplication of genera. The difference is even more striking when lists of host species are compared. Although *L. angustifrons* is reported from 17 and *L. nigra* from 22 species of Falconiformes, only 4 of these were found infested with both flies. Whether this is merely due to the vagaries of collecting cannot be decided at present. A third species, *Lynchia wolcotti,* also large, but much rarer, prefers Falconiformes as breeding hosts, since of the 8 known records, 6 are from *Accipiter, Buteo,* and *Urubitornis,* and 2 from owls. Africa likewise has a small and a large *Lynchia* almost peculiar to diurnal birds of prey: the smaller species, apparently as yet undescribed, is common on *Accipiter, Buteo,* and *Circaëtus,* but is taken occasionally on hornbills also; the larger *L. dukei* occurs on *Haliaeëtus, Gypohierax, Gymnogenys, Hieraaëtus, Milvus, Buteo,* and *Aquila.* The foregoing five flies all seem to use diurnal birds of prey as their only breeding hosts. Similar specific louse-flies of Falconiformes probably occur in the Oriental, Indo-Malayan and Australian areas, but cannot be recognized at present for want of sufficient collecting.

(2) A second group comprises flies which breed apparently on a variety of Falconiformes and on birds of other orders. A typical case is the common North American *Lynchia americana,* equally frequent on Falconiformes (*Accipiter, Buteo, Circus, Haliaeëtus, Falco,* and *Aquila*), Strigiformes and Galliformes; a combination difficult to account for, particularly as the fly strays rarely to other orders. In its original Old World habitat the pigeon-fly, *Pseudolynchia canariensis,* is often found on *Accipiter, Milvus, Neophron, Polihiërax, Gymnogenys, Buteo, Spizaëtus, Kaupifalco, Lophaëtus, Aquila, Falco,* and *Meliërax,* which seem to be as suitable for breeding purposes as the wild Columbidae. In America, *Ornithoc-*

tona erythrocephala is even more frequent on diurnal birds of prey, being known from some 29 species of the genera *Accipiter*, *Buteo*, *Elanoides*, *Leucopternis*, *Haliaeëtus*, *Falco*, *Oroaëtus*, *Herpetotheres*, *Micrastur*, *Urubitornis*, *Ictinia*, *Spizaëtus*, *Daptrius*, *Buteogallus*, and *Polyborus*. Some of these are certainly effective breeding hosts, together with Columbidae, Strigidae and Passeriformes. In Africa, *Ornithoica turdi* is often taken on *Kaupifalco*, *Elanus*, *Gypohierax*, *Lophaëtus*, *Falco*, *Accipiter*, *Buteo*, and *Machaerhamphus*, and uses these birds and some other types, particularly certain Passeriformes, for breeding.

(3) Other flies occur temporarily on Falconiformes, which they use only for feeding or shelter, in many cases following the capture of other birds, chiefly passerines, pigeons and game birds, by the predators. It is sometimes difficult to decide whether or not a given bird of prey is a true breeding host. Even the finding of flies in the nests or on juvenile birds is not by itself conclusive proof, as it may result from infested prey brought as food to the nestlings. We are particularly confronted with this problem for the two common parasites of the Old World and North America, *Ornithomyia avicularia* and *O. fringillina*. In Europe, *O. avicularia* is taken occasionally on *Accipiter*, *Buteo*, and *Falco;* and it is reported from *Circus* in Cyprus, from *Necrosyrtes* in Central Africa, and from *Accipiter* and *Uroaëtus* in Australia. Ash (1951) mentions finding *O. avicularia* on 9 out of 14 *Accipiter nisus* trapped during the fall migrating season on the island of Oeland in southern Sweden; 15 flies were taken in all, from 1 to 3 occurring on one bird. These captures were perhaps due to so-called ''live contamination'': after the hawks entered the traps to prey on trapped passerines, the disturbance may have caused some flies to leave the latter and to hide in the plumage of the intruders. *O. fringillina* occurs even more often on *Circus*, *Accipiter*, *Falco*, and *Buteo* in Europe, and on *Accipiter*, *Circus*, and *Falco* in North America. Ash (1950) found some 60 specimens (cited as *O. lagopodis*) in a nest of *Falco columbarius* in England, in July, the flies feeding on the nestlings. In the New World, *Ornithoctona fusciventris,* usually a parasite of Passeriformes, was taken on 2 species of *Accipiter, A. erythrocnemius* and *A. striatus;* and there are records of *Ornithoica vicina* from *Buteo, Falco, Accipiter, Busarellus, Micrastur,* and *Hypomorphnus,* so few, however, as compared with those from owls, that these diurnal birds of prey can scarcely be significant breeding hosts. In the Indo-Malayan and Pacific areas, the more common flies also stray occasionally to raptores: *Ornithoctona plicata* is known from *Falco,*

Accipiter, Circus, Haliastur, Aviceda, and *Hecinopernis; Ornithoica pusilla* from *Accipiter, Aviceda,* and *Buteo;* and *Ornitheza metallica* from *Falco, Accipiter,* and *Aviceda.* In the same geographical area, *Lynchia pollicipes* Ferris (1929*c*), originally described from *Accipiter* ("*Astur*"), was probably only a straggler on this type of host, as it is found more often on cuckoos, parrots and wild pigeons. There are stray records also of *Crataerina pallida* on *Buteo buteo* in Europe (Massonat, 1909), of *Ornitheza metallica* on *Machaerhamphus* in Africa, of *Ornithoctona plicata* on *Accipiter* and *Milvus* in the Mascarene Islands, and of *Ornithoctona australasiae* on *Falco* in New Guinea. The one *Hippobosca equina* from *Milvus milvus,* in the Department of Ain, France (Massonat, 1909, p. 242), was at best an accidental straggler.

The known records from Falconiformes for some other bird-flies are far too few. *Ornithomyia perfuga* was taken occasionally on *Falco* and *Accipiter* in Australia. *Ornitheza gestroi* (Rondani, 1878, p. 156), described from *Falco eleonorae* in Tunis and recorded by Gil Collado (1932, p. 40) from *Falco tinnunculus* in Morocco, possibly is not specifically distinct from *Ornitheza metallica,* a widespread Old World parasite of Passeriformes. In the Indo-Malayan Region, the only host of *Lynchia longipalpis* (= *Lynchia majuscula* J. Bequaert, 1945*b*) known thus far is a species of *Spilornis.*

10. Order Galliformes (Galli). An extensive group of medium-sized to fairly large, terrestrial, so-called game birds, little addicted to flying or perching, often gregarious, usually brooding on rather crude nests built on the ground and abandoned shortly after the eggs hatch. Though chiefly vegetarian, most species may eat a fair amount of animal matter, mainly mollusks and insects, the bill being suitable to a varied diet. When present, louse-flies are usually few on a bird and, with three notable exceptions mentioned below, belong to species having also other types of breeding hosts, from which the game birds possibly become reinfested periodically.

The family Opisthocomidae (1. Neotropical), or the hoatzin, has no known bird-fly.

In the Megapodiidae (10. East Indies to Australia), or brush turkeys, there are a few, possibly stray records of *Ornithoctona plicata* from *Megapodius* in Queensland and the Bismarck Archipelago. Austen (1903) referred to *Lynchia* (*Ornithophila*) *simplex* a fly taken in Queensland on *Alectura lathami,* and I have seen it from the same host.

The Cracidae (38. Neotropical) have a specific parasite, *Olfersia* *coriacea,* on the tropical American guans and their allies (*Crax, Penelope,* and *Ortalis*). The fly occurs also on the wild ocellated turkey. In eastern Brazil, it is occasionally found on domestic turkey, which may have become there a newly acquired breeding host; but the one record from a tinamou was almost certainly due to straggling. The common American *Ornithoctona erythrocephala* and *O. fusciventris* sometimes stray to *Chamaepetes, Penelope,* and *Penelopina.* There is also one stray record of *Stilbometopa ramphastonis* from *Pipile jacutinga. Lynchia penelopes,* the type of the genus *Lynchia,* was described from *Ortalis canicollis* in Argentina, but unfortunately is at present unrecognizable.

The Phasianidae (190. Cosmopolitan; including Tetraonidae and Numididae of Peters) harbor several common parasites. In western North America, two important flies are specific parasites of native gallinaceous birds: *Stilbometopa impressa* is common on quail (*Lophortyx* and *Oreortyx*) and *Lynchia hirsuta* on quail (*Lophortyx*), grouse (*Dendragapus*), and sage hen (*Centrocercus*); the few occurrences on other hosts are clearly accidental. In Europe and North America, grouse, quail and related birds (*Colinus, Lagopus, Bonasa, Tetrao, Dendragapus,* and *Canachites*) are frequently infested with *Ornithomyia fringillina* (= *lagopodis*); in North America *Lynchia americana* occurs likewise on *Bonasa, Pedioecetes,* and *Colinus;* both flies seem to use game birds as true breeding hosts, together with either song birds or birds of prey. In the Indo-Malayan Region, *Lynchia* (*Ornithophila*) *maquilingensis* is evidently a specific parasite of Phasianidae, as it was taken on *Haematortyx* in Borneo (Ferris, 1926, p. 282) and on wild fowl, *Gallus gallus bankiva,* in Java (Schuurmans Stekhoven and Hardenberg, 1938, p. 35); according to specimens collected by Dr. H. S. Fuller at Myitkyina in 1945, it is common on wild fowl, *Gallus g. gallus,* in Burma. Other bird-flies have been reported from the several introduced races of the Asiatic pheasant, *Phasianus colchicus: Ornithomyia avicularia* and *O. fringillina* in Europe; *Ornithoctona erythrocephala* and *Lynchia americana* in North America; but it is doubtful whether they are more than temporary strays. Flies have never been taken on wild pheasants in their native Asiatic haunts. In various parts of the World bird-flies stray occasionally to the domestic hen: *Ornithomyia avicularia* and *O. fringillina* in Europe; *Pseudolynchia canariensis, Stilbometopa impressa* and *Ornithoica vicina* in North America; *Stilbometopa podopostyla* in South America (Paraguay); *Ornithoctona plicata* in the Pacific

Islands (in this case on birds gone feral). According to Schwartz and Schwartz (1951, p. 301), in the Hawaiian Islands, *Ornithoica vicina* is sometimes taken on the introduced ring-necked pheasant, *Phasianus colchicus torquatus,* Japanese quail, *Coturnix coturnix japonica,* and even jungle fowl (feral *Gallus gallus*). In America, *Microlynchia pusilla,* normally found on Columbidae, sometimes strays to quail (*Callipepla*); while the common *Ornithoctona erythrocephala* occurs now and then on *Dactylortyx* and *Odontophorus.* In Africa, *Pseudolynchia canariensis* is rarely taken on francolin (*Pternistis*) and guinea fowl (*Numida*); *Lynchia pilosa,* the specific fly of bustards, strays occasionally to francolin (*Francolinus*) and sandgrouse (*Pterocles*); *Ornitheza metallica* may occur on *Coturnix* and *Ornithoica turdi* on *Guttera.* In Europe, the gray partridge, *Perdix perdix,* has been found infested with stray *Ornithomyia avicularia, O. fringillina,* and *Ornitheza metallica;* but no flies have been taken on it in America since it was introduced. Finally, there is one European published record of *Ornithomyia avicularia* from the domesticated peacock, *Pavo cristatus,* a bird introduced from India.

In the Meleagridae (2. America), or turkeys, there are well-substantiated records of *Lynchia americana* from the North American wild turkey, *Meleagris gallopavo silvestris,* evidently a true breeding host of this fly. *Olfersia coriacea,* the specific fly of American Cracidae, perhaps breeds also on the wild ocellated turkey, *Agriocharis ocellata;* but on the domestic turkey it may be temporary or accidental only. In southern Brazil, there is one record of *Stilbometopa podopostyla* from domestic turkey.

11. Order Gruiformes (Grues). A fairly numerous and ecologically rather disparate group of small to moderately large birds, some aquatic (such as the cranes), others ground birds (such as the bustards and rails). The nests are loosely constructed, placed on the ground, in dry or damp places. The food is very varied. The plumage is similar to that of the Ciconiiformes, though perhaps not as long and dense.

Of the 11 families included, 8 have no known fly parasites: Cariamidae (2. Neotropical), Psophiidae (3. Neotropical), Aramidae (1. Neotropical), Heliornithidae (3. Tropicopolitan), Rhynochetidae (1. New Caledonia), Mesoenatidae (3. Madagascar), Turnicidae (16. Old World tropics), and Gruidae (14. Old World).

In the Eurypygidae (1), the South American sun bittern, *Eurypyga helias,* has a stray record of *Ornithoctona erythrocephala.*

The Rallidae (132. Cosmopolitan), or rails, are more interesting. In America, *Lynchia holoptera* is a specific parasite of *Rallus, Coturnicops,* and *Aramides;* although there is one record from a tinamou (*Rhynchotus*), evidently a straggler or a contamination. The flightless rails of Gough Island (*Porphyriornis comeri*) and of Tristan da Cunha (*Atlantisia rogersi*) are breeding hosts of *Ornithomyia remota,* a fly also common on various Passeriformes both there and on the South American continent. In North America, there are a few stray records of *Lynchia albipennis* from *Porphyrula, Porzana* and *Gallinula;* in Europe *Ornithomyia avicularia* has been reported from *Gallinula* and *Rallus,* and *O. fringillina* from *Crex,* no doubt also as stragglers. The one reported find of *Ornithoica pusilla* on a species of *Rallus* in Samoa was possibly accidental.

The Otitidae (23; also called Otidae. Old World), or bustards, have in Africa a highly specific fly, *Lynchia pilosa,* known from several species of *Neotis, Choriotis, Afrotis, Eupodotis,* and *Lissotis;* there are a few stray records from francolin (*Francolinus*) and sandgrouse (*Pterocles*). It is surprising that no louse-flies were ever taken on bustards in Europe and Asia.

12. Order Charadriiformes (Laro-Limicolae). An extensive group of small to large birds, ecologically similar to the Ciconiiformes, being all aquatic or shore birds. Their plumage is, however, rather short as compared to that of most waders, which may explain why they are not particularly attractive to bird-flies. With the possible exceptions of *Olfersia aenescens* and *O. fossulata* on some of the Laridae, they seem to harbor only strays of species commonly breeding on other birds.

No records are known from the following 4 families: Thinocoridae (4. South America), Chionididae (2. Antarctic), Dromadidae (1. Indian Ocean), and Glareolidae (16. Old World).

In the Jacanidae (7. Pantropical), or jacanas, there is one record of *Lynchia albipennis,* the common fly of waders, from the African *Actophilornis africana.*

In the Haematopodidae (6. Cosmopolitan), or oystercatchers, *Ornithomyia fringillina* was taken as a stray on *Haematopus ostralegus* in Europe.

The Charadriidae (152. Cosmopolitan; including Rostratulidae, Scolopacidae, Recurvirostridae, and Phalaropodidae of Peters) comprise the plovers, sandpipers, phalaropes, avocets and their allies. Although there are now several records of *Ornithomyia avicularia* and *O. fringillina* from *Squatarola, Vanellus, Pluvialis, Scolopax, Charadrius, Calidris, Numenius, Tringa, Actitis,* and

Capella, in Europe, the exact relations of the flies of these hosts should be more carefully investigated before including these birds among the regular breeding hosts. In North America, *Ornithomyia fringillina* was taken once on a woodcock (*Philohela*) and there are two stray records of *Lynchia albipennis* from *Tringa.* In Africa, *Lynchia albipennis* was taken as a stray on *Xiphidiopterus albiceps* and I have seen a *Hippobosca equina* taken on *Erolia* in Morocco. There is one record of *Ornithoctona plicata* from *Capella megala* in the Far East.

The Laridae (89. Cosmopolitan; including Stercorariidae and Rhynchopidae of Peters), the gulls, terns, skuas and skimmers, have yielded only a few stray *Ornithomyia fringillina* on *Larus* in Europe and North America and on *Stercorarius* in Europe; and one stray *Lynchia albipennis* on *Larus* in the Galapagos. In addition, *Olfersia aenescens,* a common parasite of the Pelecaniformes, particularly of tropic birds (*Phaëthon*) and boobies (*Sula*), is taken sometimes on sooty terns (*Sterna fuscata*) and noddies (*Anous*). As in the case of shearwaters and petrels, sooty terns and noddies may be only accidental, not true breeding hosts. *O. aenescens* perhaps strays to them in rookeries also occupied by boobies, such places often swarming with newly-emerged flies. Whether a similar explanation will account for the reported occurrences of *Olfersia fossulata* on Belcher's gull, *Larus belcheri,* and Inca tern, *Larosterna inca,* cannot be decided at present.

For the Alcidae (22. Holarctic), the auks and murres, I can find only one stray record of *Lynchia americana* from Brunnich's murre, *Uria l. lommia,* in Quebec.

In the Burhinidae (9. Cosmopolitan), or thick-knees, I have seen a stray specimen of *Pseudolynchia rufipes* from an African *Burhinus.*

13. Order Columbiformes (Columbae). Pigeons and their close allies are among the most favored hosts of hippoboscids. They are fair-sized birds, either mainly arboreal or more or less terrestrial, usually building rather crude and untidy nests, some distance above the ground, frequently in trees or on rocky ledges. They are essentially frugivorous or granivorous, even the arboreal species often feeding on the ground. Many species are gregarious and migratory. Their dense and smoothly imbricated plumage offers excellent shelter for many ectoparasites.

One family, the Raphidae (3), or dodos of the Mascarene Islands, has become extinct within the past 400 years.

In the Pteroclidae (16. Ethiopian and Palearctic), or sandgrouse, there are now four records from *Pterocles,* two of *Pseudolynchia canariensis* in Arabia and West Africa, and two of *Lynchia pilosa* in Morocco and South West Africa, presumably all accidental occurrences.

The Columbidae (289. Cosmopolitan), or true pigeons, are of unusual interest to the student of the Hippoboscidae. They not only harbor a fair number of species of flies, but some of these use pigeons as their main breeding hosts. The best known of these is *Pseudolynchia canariensis* (= *Lynchia maura*), the nearly cosmopolitan fly of domestic pigeons; but this fly, while restricted to domestic pigeons in the New World, uses several wild Columbidae as regular breeding hosts in the Old World (*Columba, Treron, Streptopelia,* and *Turtur*). Other aspects of the host-parasite relation of *P. canariensis* are discussed elsewhere in this work. Domestic pigeons occasionally harbor stragglers of other local bird-flies, such as *Ornithomyia avicularia* in Europe and Tasmania, and *Microlynchia pusilla, Stilbometopa podopostyla* and *Ornithoctona erythrocephala* in the New World. The wild, native Columbidae of the New World frequently harbor the strictly American *Ornithoctona erythrocephala* (on *Columba, Leptotila, Oreopeleia, Claravis, Geotrygon, Zenaida, Zenaidura,* and *Columbigallina*), *Microlynchia pusilla* (on *Leptotila, Oreopeleia, Zenaidura, Nesopelia, Columbigallina* and *Scardafella*), and more rarely *Stilbometopa podopostyla* (on *Zenaida, Scardafella,* and *Zenaidura*); these three species are not restricted to Columbidae, but breed also on other types of birds. In the Oriental Region and Oceania, *Ornithoctona plicata* is a frequent and apparently normal parasite of wild Columbidae (*Ptilinopus, Leucotreron, Ducula, Phapitreron, Chalcophaps, Macropygia, Treron, Streptopelia, Reinwardtoena, Gallicolumba,* and *Didunculus*), although some other types of birds seem to be equally effective breeding hosts. In the same region, *Ornithoctona australasiae* is not so well known, but has been recorded from *Ducula* and *Sphenurus; Ornithoica pusilla* is known to occur on *Caloenas, Leucotreron, Gallicolumba, Ptilinopus,* and *Ducula, Lynchia pollicipes* on *Caloenas,* and *Ornitheza metallica* on *Gallicolumba.* Other species stray now and then to wild pigeons, such as *Ornithomyia avicularia* to *Columba livia, C. oenas, C. palumbus,* and *Streptopelia turtur,* in Europe; the smaller *O. fringillina* seems to avoid wild as well as domestic pigeons. For Africa, I have one record of *Ornithoctona laticornis* (= *platycera*) from *Columba* and another of *Ornithoica turdi* from *Treron.* The recorded occurrence of *Myiophthiria reduvioides,* a specific fly of swifts, on *Geopelia,* in the Philippines, is perhaps not reliable.

14. Order Psittaciformes (Psittaci). The Psittacidae (316. Pantropical and New Zealand), or parrots, are strictly arboreal and almost wholly frugivorous. The present scarcity of fly records, notwithstanding the frequent abundance and gregariousness of these birds, is presumably due to inadequate collecting. So far as known, no species is restricted to parrots, although most of the recorded flies use them as true breeding hosts. In America, *Ornithoica vicina* is reported from *Amazona,* and *Ornithoctona erythrocephala* from *Pionus, Amazona,* and *Aratinga.* In the East Indies, *Ornitheza metallica* was taken on *Loriculus* and *Micropsitta; Lynchia pollicipes* on *Prioniturus, Kakatoë,* and *Lorius; Ornithoica pusilla* on *Loriculus;* and *Ornithoctona plicata* on *Coracopsis* and *Tanygnathus.* In Australia, *Ornithomyia avicularia* is a frequent parasite of *Neophema, Glossopsitta, Trichoglossus, Platycercus,* and *Calyptorhynchus;* and there is one record each of *Ornithomyia perfuga* from *Platycercus* and of *Lynchia* sp. from *Kakatoë.* Finally, *Ornithoica pusilla* was found in the Hawaiian Islands on an introduced Australian parrot, *Melopsittacus undulatus.* No fly has as yet been recorded from an African parrot.

15. Order Cuculiformes (Cuculi). Medium-sized, chiefly tropical birds, ecologically similar to the Passeriformes, some frugivorous, other insectivorous. Most of them build nests similar to those of the song birds. Some species are parasitic, depositing their eggs in the nests of other birds, in which case the parasitic bird may be expected to harbor sometimes the same louse-flies as its unsuspecting host or victim. In line with the foregoing features, the Cuculiformes have no specific hippoboscids of their own.

In the Musophagidae (19. Africa), or plantain eaters, the common African *Ornithoica turdi* occurs rather frequently on *Tauraco, Musophaga, Ruwenzornis,* and *Crinifer,* these birds being apparently true breeding hosts. In addition, there is one stray record of *Ornitheza metallica* from *Corythaeola,* and there are two reports of *Pseudolynchia canariensis* from *Crinifer.*

The Cuculidae (128. Cosmopolitan), or true cuckoos, are by no means all parasitic, this being rather the exception.[20] In Europe, *Cuculus canorus* occasionally harbors *Ornithomyia fringillina* and *O. avicularia;* I have seen *Pseudolynchia canariensis* from the same bird in Cyprus. In North America, *Microlynchia pusilla* is so often found on the roadrunner, *Geococcyx californicus,* that this bird should be regarded as one of its true breeding hosts. In tropical America, there are stray records of *Ornithoica vicina* and *Lynchia nigra* from *Piaya; Ornithoctona erythrocephala* was taken on both *Piaya* and (in the Antilles) on *Saurothera.* In Africa, *Pseudolynchia canariensis* is found sometimes on *Clamator, P. rufipes* on *Centropus, Ornithoica turdi* on *Centropus* and *Clamator,* and *Ornitheza metallica* on *Cuculus.* In the Pacific Islands, both *Lynchia pollicipes* and *Ornithoica pusilla* are recorded from *Centropus.* There are also a few records of *Ornithoctona plicata* from *Eudynamys* in Australia and *Rhamphococcyx* in the Philippines.

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[20] Of the genera mentioned in the present discussion, only *Cuculus* and *Clamator* contain parasitic species.

16. Order Strigiformes (Striges). The owls, or Strigidae (134. Cosmopolitan; including Tytonidae of Peters), are mostly large or medium-sized birds, chiefly nocturnal and predatory on small mammals and passerine birds. The long, soft, dense plumage offers ideal shelter for ectoparasites, while the broad, short, hooked bill is ill-suited for preening. Both features no doubt account for the frequency and abundance of certain louse-flies on owls, which are among the most important breeding hosts of the Hippoboscidae. Their host-parasite relations parallel closely those of the Falconiformes, although the species of flies are not necessarily the same for both orders. Three main degrees of specificity may again be recognized.

(1) According to present knowledge, only one species, *Lynchia fusca,* of the New World, appears to be a fairly specific parasite of owls, almost to the exclusion of other birds. It has been taken repeatedly on at least 15 species of *Asio, Aegolius, Bubo, Ciccaba, Glaucidium, Otus, Rhinoptynx, Pulsatrix, Speotyto,* and *Tyto.* There are some 20 individual records for *Bubo virginianus* and about the same number for *Otus asio.* In contrast, there are not more than half a dozen records from diurnal birds of prey (*Accipiter, Buteo, Haliaeëtus,* and *Micrastur*); the one or two supposed occurrences on other types of birds are almost certainly erroneous.

(2) In most parts of the World, some species of flies occur so frequently on owls that they must regularly breed on these birds, even though they have additional breeding hosts of other orders. In Europe, the two common parasites of song birds, *Ornithomyia fringillina* and *O. avicularia* are often taken on owls: *O. fringillina* on *Asio, Bubo, Otus, Strix,* and *Surnia;* and *O. avicularia* on *Asio, Athene, Strix,* and *Tyto;* Corbin (1901) claims that *O. avicularia* is more common in parts of England on the long-eared owl, *Asio*

otus, than on passerines. I have seen *Ornithoica turdi* from *Strix aluco* in Italy. In North America, *Lynchia americana* occurs frequently and in numbers on *Asio, Bubo, Otus, Strix,* and *Tyto,* and there is some evidence that owls may be among its chief permanent hosts in winter; *Ornithomyia fringillina* likewise is by no means rare on *Asio, Glaucidium, Bubo,* and *Otus.* In the New World also, *Ornithoica vicina* is sometimes abundant on owls, being recorded from *Aegolius, Asio, Bubo, Ciccaba, Glaucidium, Otus, Pseudoscops, Strix,* and *Tyto;* owls are important breeding hosts of this fly and perhaps act as a permanent reservoir during the winter. In Australia, *Ornithomyia avicularia* occurs on *Otus* and *Ninox, O. perfuga* on *Ninox,* and *Ornitheza metallica* on *Tyto.* In the Old World, the pigeon-fly, *Pseudolynchia canariensis,* is taken occasionally on *Ketupa, Asio, Otus, Athene,* and *Bubo,* but is rarer on owls than on diurnal birds of prey. In Africa, *Ornithoica turdi* was taken on *Otus, Asio, Bubo,* and *Ciccaba;* and, in the Indo-Pacific area, *Ornithoica pusilla* on *Ninox, Pseudoptynx, Tyto,* and *Asio;* but the records are too few to be more than suggestive.

(3) Stray records from owls are available for several hippoboscids. No doubt they are frequent because the large and heavily feathered body of these birds offers a ready temporary shelter for any fly forced to leave its normal host. In the Old World, there are records of *Ornithoctona plicata* from *Asio* and *Tyto;* of *Ornitheza metallica* from *Athene, Ninox, Otus, Tyto,* and *Asio;* of *Pseudolynchia rufipes* from *Athene, Bubo, Ciccaba,* and *Tyto;* and there is even one record of *Ornithomyia biloba* from *Bubo.* In America, *Ornithoctona erythrocephala* has been taken on *Tyto, Pseudoscops, Otus, Scotiaptex, Asio,* and *Glaucidium; Lynchia albipennis* on *Rhinoptynx* and *Tyto; L. angustifrons* on *Ciccaba* and *Glaucidium; L. nigra* on *Rhinoptynx;* and *L. wolcotti* on an unidentified owl in Costa Rica. There is one record of *Ornithomyia remota* from *Glaucidium,* in Chile, and another of *Olfersia fossulata* from *Tyto,* in Peru. The scarcity on owls of some of these flies, particularly *L. angustifrons* and *L. nigra,* is remarkable in view of their abundance on diurnal birds of prey. Accidental occurrences of *Hippobosca equina* on *Athene* and *Glaucidium,* in Europe, are discussed later.

17. Order Caprimulgiformes (Caprimulgi). This small group of mostly nocturnal insectivorous birds, contains the nightjars, goatsuckers, and their allies. The body is very thickly clothed in soft, long contour feathers, an ideal safe retreat for flies; while the broad and short bill is little suited to catching quick-moving parasites in the plumage. Most species build very crude or no nests.

Three of the 5 families included have no known louse-flies: Steathornithidae (1. Neotropical), Aegothelidae (8. Indo-Malayan, Australia), and Nyctibiidae (5. Neotropical).

In the Podargidae (12. Indo-Malayan, Australia), or frogmouths, there is one stray record of *Ornithoica pusilla* from *Batrachostomus;* and I have seen specimens of *Ornithomyia perfuga* taken from *Podargus strigoides,* in Australia.

For the Caprimulgidae (67. Cosmopolitan), or goatsuckers and allies, the available records, though scant, indicate clearly that these birds have their own specific louse-flies. In the New World, *Pseudolynchia brunnea* has been found repeatedly on *Chordeiles, Caprimulgus, Hydropsalis, Nyctidromus,* and *Phalaenoptilus;* but once only on another type of bird (*Hylocichla*), either as a stray or perhaps due to a contamination. The specificity of the African *Pseudolynchia rufipes* is not as strict; but it occurs frequently on *Caprimulgus, Scotornis, Macrodipteryx,* and *Semeiophorus,* which are its breeding hosts together with owls and perhaps other birds. In Australia, *Ornithomyia avicularia* was taken on *Eurostopodus,* possibly as a stray. In America, *Microlynchia pusilla* sometimes strays to *Caprimulgus,* and *Ornithoctona erythrocephala* to *Chordeiles* and *Siphonorhis.* In Europe, Gil Collado (1947, p. 220) reported the pigeon-fly, *Pseudolynchia canariensis* (= *P. maura*), from the goatsucker (''chotacabras''), *Caprimulgus europaeus,* in Spain; this record may have been based on *Pseudolynchia rufipes,* which I have seen from *C. europaeus* in Southern Rhodesia.

18. Order Apodiformes (Macrochires). This comprises the two families Apodidae (79. Cosmopolitan; including Hemiprocnidae of Peters) and Trochilidae (319. American).

Thus far the only louse-fly taken on one of the Trochilidae, or hummingbirds, is a stray *Ornithoctona* (*Ornithopertha*) *nitens* from *Phaethornis,* in Nicaragua.

The Apodidae, or swifts, are frequently infested with flies which are of absorbing interest, not only because they are among the the most strictly specific Hippoboscidae, but also owing to their unusual adaptive features. Swifts are mostly small birds, of predominantly aërial habits, capable of long-sustained flight, as they catch their insect food on the wing. Most species are unable to perch. When not nesting, some of them must stay aloft for the major part of the day, at one stretch. They include possibly the fastest flying birds for their size, sometimes reaching speeds of 70 to 100 miles an hour. The narrow, pointed wings, very long in proportion to the small body, and the often forked tail (the fork capable of opening and closing) are clearly correlated with aërial life. The contour feathers are rather coarse and stiff, densely pressed together, so as to form an even and smooth outer surface. Added to the peculiar build of the body, particularly of the head, they produce a "streamline" shape offering the least possible resistance to the air. All swifts tend to be gregarious, particularly during their seasonal migrations, and they often nest in extensive and compact colonies. Nesting behavior varies within the order. The common European swift, *Apus apus,* broods in holes or crevices, usually between rocky ledges, frequently under the eaves of buildings where the bird is associated with Man; it does little or no actual nest building; it roosts on the nest, but during the day it stays away for long stretches, feeding the young only every three hours or at longer intervals. Other Apodidae, however, such as the American *Aëronautes* and *Nephoëcetes* and the Old World *Collocalia* (or salanganes), build carefully constructed and durable nests in high, inaccessible, sheltered places, usually cemented to rocks. The birds return to the same nesting sites year after year.

These morphological and ecological peculiarities of the swifts are closely integrated with the many equally striking features of their louse-flies, the most specialized of the Ornithomyiinae, or louse-flies of birds. The specific swift flies belong to two genera, *Crataerina* and *Myiophthiria* (including *Brachypteromyia,* which is at most of subgeneric value). All have lost the power of flight, the wings being more or less reduced in size. In *Crataerina,* most of the membrane has disappeared, the wing being moderately narrowed at the base and very much so apically, while retaining its full length or even tending to be more drawn out at the tip; in *Myiophthiria,* the entire wing is reduced to a very short, oval pad. In addition, in both genera the head is considerably longer than usual, with smaller eyes and without ocelli; the thorax is greatly flattened, with obsolescent sutures and with a deep anterior notch in which the head fits snugly, the occipital margin overlapping the anterior slope of the notum; the unusually strong legs are provided with long, deeply split (seemingly three-pronged) claws. Body and legs are covered with many long, stiff bristles, used not only as tactile sensoria to guide the fly's movements within the dark plumage, but also to help it adhere to the feathers like a burr. All these features give the flies a decided spider-like appearance and are clearly correlated with permanent ectoparasitic life on hosts travelling at high speed through the air. In particular, the atrophy of the wings decreases the risk of the fly's being blown off the host; while wings are no longer of much use for reaching a new host with birds spending so much of their life in mid-air and away from the nest. Speiser (1905*b*) suggested that the gregarious nesting habits of the swifts might have induced the subapterous condition of their flies. It seems doubtful that this could have been a sufficiently powerful incentive to initiate the evolutionary changes involved. Other types of birds which nest in large colonies, such as the marine Procellariiformes, are regularly and profusely infested with specific hippoboscids, which have retained fully-developed wings and are active fliers. The predominantly aërial habits of the hosts were, in my opinion, the determining factor in producing the aberrant *Crataerina* and *Myiophthiria* of the swifts. A similar, parallel evolution led to the peculiar, specific louse-flies of the swallows (Hirundinidae), to be discussed later, which have not progressed quite as far as the swift flies.

Of the 17 genera recognized by Peters in the Apodidae, only 5 have thus far yielded specific hippoboscids. No doubt this is due to insufficient collecting, these birds being among the most difficult to obtain for the study of ectoparasites, particularly in the tropics. In the Old World, so far as known at present, only species of *Apus* are used as breeding hosts by the genus *Crataerina,* the species of which appear to have been over-multiplied. The following are here accepted at their face value, pending a much needed revision: *C. pallida* and *C. melbae* in Europe and Africa; *C. longipennis* and *C. propinqua* in Asia; and *C. acutipennis* in Africa and Ceylon. According to Schneider-Orelli (1937, p. 7), in Switzerland, *C. pallida* occurs both on the chimney swift, *Apus apus,* and the alpine swift, *Apus melba,* while *C. melbae* is restricted to the alpine swift. It is remarkable that *Crataerina seguyi,* the only New World species of the genus, is a specific parasite of swallows, not of swifts. Although the evolution of the flies of the swallows and swifts was evidently simultaneous and ran parallel in both groups, it ignored the affinities of the hosts. *Myiophthiria* occurs in the Indo-Malayan and Pacific areas, and also (as subgenus *Brachypteromyia*) in the New World. The Old World species are apparently restricted to *Collocalia,* the salanganes or swifts with edible nests: *M. reduvioides* is known from *C. troglodytes, C. spodiopygia,* and *C. vanikorensis;* I have seen *M. lygaeoides* from *C. brevirostris unicolor* in Ceylon. Kishida (in Esaki, 1932) described his "*Brachypteromyia namakurai*" from *Hirundo,* but the record is at present unreliable. In

North America, *Myiophthiria* (*Brachypteromyia*) *fimbriata* was taken on *Aëronautes* and *Nephoëcetes.* In South America, *M.* (*B.*) *neotropica* is known only from *Aëronautes.*

It is difficult to decide how trustworthy most stray records are of other Hippoboscidae from swifts, either published or in collections. *C. pallida* of the swifts and *Stenepteryx hirundinis* of the swallows, for instance, are very similar and often confused, and some observers are even careless about differentiating between swallows and swifts. In Europe, *S. hirundinis* is said to occur now and then on *Apus.* There are also stray records of *Ornithomyia fringillina* (more probably *O. biloba*) from *Apus* in Europe, and of *Pseudolynchia rufipes* from *Apus* in Africa. Finally, *Ornitheza metallica* is the only fly ever reported from the peculiar Indo-Malayan genus *Hemiprocne,* a record no doubt based on a stray specimen (J. Bequaert, 1941*b,* p. 260).

19. Order Coliiformes (Colii). This order contains the one small family Coliidae (6), the mousebirds or colies, with one genus, *Colius,* restricted to the Ethiopian Region. Thus far there is only one stray record of *Ornitheza metallica* from *Colius indicus* in South Africa.

20. Order Trogoniformes (Trogones). The one family Trogonidae (35), or trogons, found in all tropical areas of the World, comprises fairly large, arboreal, frugivorous or insectivorous birds of the rain forest. With one exception, the flies known from them are more often found on other types of birds, being usually common parasites of song birds or pigeons in the same general area.

Ornithoctona (*Ornithopertha*) *nitens,* of tropical America, appears to be a specific fly of trogons, since 8 of the 10 known host records are from *Trogon* and *Pharomachrus,* the remaining records being from a wild pigeon and a humming bird.

In the New World also, there are two stray records of *Ornithoctona erythrocephala* from *Pharomachrus* and *Temnotrogon,* another of *Stilbometopa ramphastonis* from *Trogon,* and a third of *Lynchia angustifrons* from *Trogon.* In Africa, I know only stray occurrences of *Ornithoctona laticornis* (= *platycera*) and *Ornitheza metallica* on *Apaloderma.* In the East Indies, *Ornithoctona plicata* and *Ornithomyia avicularia* are reported as strays from *Harpactes.*

21. Order Coraciiformes (Coraciae). A group of birds of varied appearance and habits, which seem to share few ecological features. Of the 7 families included, only one, the Todidae (5. Antilles), has no known parasitic fly.

The Coraciidae (17. Old World tropics; including Leptosomatidae of Peters), or rollers, seem to harbor only an occasional stray hippoboscid in Africa: *Ornithoica turdi* on *Coracias* and *Eurystomus; Pseudolynchia canariensis* on *Coracias;* and *Ornitheza metallica* on *Eurystomus. Ornithoctona idonea* Falcoz (1930) was described from *Leptosomus discolor,* in Madagascar.

The Alcedinidae (87. Cosmopolitan), or kingfishers, are of greater interest. Their strictly fish-eating habits and resulting fondness of the vicinity of water set them apart from most other land birds. They usually nest in tunnels in banks of rivers, a few species also in holes in arboreal termitaria. They are often infested with flies, which no doubt in some cases use them as regular breeding hosts, although they have no strictly specific fly. In the Bismarck Archipelago, New Hebrides, and neighboring Pacific Islands (Carolines, Samoa), *Ornithoica pusilla* is very common on *Halcyon;* I am told by the collectors that one of these kingfishers is hardly ever seen without at least one fly. In the same general region, *O. stipituri* also occurs on *Halcyon.* In the Indo-Malayan area, *O. pusilla* has been taken on *Ceyx, Dacelo,* and *Todiramphus;* the closely related *Ornithoica philippinensis* was found on *Ceyx; Ornitheza metallica* is common on *Halcyon;* and there are records of *Ornithoctona plicata* from *Halcyon* and of *O. australasiae* from *Lacedo.* In Africa, *Ornithoica turdi* strays sometimes to *Halcyon* and *Ornithoctona laticornis* (= *platycera*) to *Ispidina.* Surprisingly few flies have been collected from New World kingfishers: both *Ornithoctona erythrocephala* and *Ornithomyia fringillina* are reported from *Megaceryle* in North America; perhaps the scarcity of records is due in this case to insufficient collecting. In Australia, *Ornithomyia perfuga* appears to be a fairly regular parasite of the laughing jackass or "kookaburra," *Dacelo n. novaeguineae* (= *D. gigas*), occurring even on the nestlings (Hindwood, 1947, p. 128; as *O. avicularia*); but this fly infests also a variety of birds of other orders.

The Meropidae (25. Old World tropics), or bee eaters, have yielded only stray fly records. In Africa, *Ornitheza metallica* and *Ornithoica turdi* were taken on *Melittophagus* and *Ornitheza metallica* also on *Aërops.* In the East Indies, there is one record of *Ornitheza metallica* from *Merops.*

The Momotidae (8. Neotropical), or motmots, have thus far yielded only a few stray records of *Ornithoctona erythrocephala* and *O. fusciventris* from *Momotus,* as well as of *Lynchia angustifrons* from *Momotus* and *Baryphthengus.*

In the Upupidae (7. Old World, including Phoeniculidae of Peters), or hoopoes, I can find only a single capture of *Ornitheza metallica* on *Upupa epops* in Europe.

The Bucerotidae (45. Old World tropics), or hornbills, are a small family of fairly large, frugivorous or insectivorous birds, nesting in hollow trees. They are frequently infested with flies and some species no doubt use them as regular breeding hosts. Possibly some hippoboscids may even be specific of hornbills; but the available evidence is insufficient. In Africa, a small species of *Lynchia* has been taken on *Ceratogymna,* and *Ornithoica turdi* on *Tockus.* In the East Indies, *Ornithoica unicolor* occurs on *Aceros, Penelopides* and *Buceros; Lynchia dioxyrhina* was described from *Aceros* and *L. bicorna* (probably a synonym of *dioxyrhina*) from *Penelopides; Lynchia sarta* is reported from *Buceros,* and *Ornithoctona plicata* from *Penelopides.*

22. **Order Piciformes (Pici).** This order comprises the woodpeckers, flickers, wrynecks, toucans, honey-guides, barbets, puffbirds, and their allies, a mixed assemblage of ecologically diverse types. All are arboreal land birds, usually nesting above the ground and often in hollow trees. The diet varies from strictly insectivorous to mixed or frugivorous; the honey-guides eat also wax and honey. They are on the whole little sought after by louse-flies, none of which are at present known to be specific parasites.

I can find no hippoboscid record for any member of the Bucconidae (32. Neotropical), or puffbirds; Galbulidae (14. Neotropical), or jacamars; and Indicatoridae (12. African), or honey-guides.

The Picidae (210. Cosmopolitan), or woodpeckers, wrynecks, piculets and flickers, carry hippoboscids rather frequently, but always sporadically and of species found commonly on other types of birds. In Europe, *Ornithomyia avicularia* is reported from *Dendrocopos* and *Picus,* and *O. fringillina* from *Jynx* and *Dryocopus.* In North America, *Ornithomyia fringillina* is taken sometimes on *Colaptes, Sphyrapicus, Dendrocopos,* and *Picoides; Ornithoica vicina* on *Dendrocopos; Ornithoctona erythrocephala* on *Sphyrapicus;* and *Lynchia americana* on *Dryocopus.* In the Antilles, *Ornithoctona erythrocephala* has also been taken on *Melanerpes* and *Linneopicus.* In South America, there are a few records of *Ornithomyia remota* from *Colaptes* and of *Lynchia angustifrons* from *Veniliornis.* In Africa, *Ornitheza metallica* occurs as a stray on *Mesopicos* and *Campethera;* and both *Ornithoica turdi* and *Or-*

nithoctona laticornis (= *platycera*) stray to *Dendropicos.* In the Indo-Pacific area, *Ornithoica pusilla* is reported from *Chrysocolaptes,* and *Ornithoctona plicata* from *Dryocopus* and *Mulleripicus.* Most probably the Picidae are never true breeding hosts, but merely pick up flies emerging from puparia deposited by parasites of other birds that nested previously in the same sites.

The Ramphastidae (37. Neotropical), or toucans, are sometimes infested with bird-flies; but it is as yet a moot question whether they are ever true breeding hosts. None of their flies are specific parasites. *Lynchia angustifrons* occurs on *Pteroglossus* and *Ramphastos;* and *Ornithoica vicina, Ornithoctona erythrocephala,* and *Stilbometopa ramphastonis* on *Ramphastos.* The name notwithstanding, *S. ramphastonis* occurs more often on other birds, only 2 of the 9 known host records being from toucans.

The Capitonidae (76. Cosmopolitan in the tropics), or barbets, have yielded few records, apparently all based on strays. In Africa, *Ornitheza metallica* was found on *Gymnobucco* and *Lybius.* In India, *Lynchia trita* was described from *Megalaima. Lynchia pollicipes,* which I have seen from *Megalaima* in Burma, may be a synonym of *L. trita.* In the Philippines, there is one record of *Ornitheza metallica* from *Megalaima* also.

23. Order Passeriformes (Passeres). The perching or song birds comprise over 5000 species, that is, over one-half of all living birds. Although their habits and habitus vary greatly, most of them are arboreal, but often feed on the ground (except the Hirundinidae). Some have a mixed diet; many are mainly granivorous and others more nearly insectivorous. They usually build carefully constructed, sometimes elaborate nests in dry situations. Many migrate at definite seasons away from their breeding areas, to return to them later, at which times they usually congregate in flocks, often of mixed species. They are frequently preyed upon by diurnal and nocturnal birds of prey. The partly terrestrial habits bring them sometimes in the environment frequented by gallinaceous birds (Galliformes) and Columbidae. These several ecological features go a long way to explain the low degree of specificity of their hippoboscid parasites, as well as the ease with which their flies stray to unusual hosts.

Of the 50 families recognized by Mayr and Amadon (1951), the following 16 have thus far no recorded flies: Eurylaimidae (14. Old World tropics), or broadbills; Conopophagidae (10. Neotropical), or ant-pipits; Philepittidae (4. Madagascar), or philepittas; Xenicidae (4. New Zealand), or New Zealand wrens; Pipridae (59.

New World, mainly tropical), or manakins; Phytotomidae (3. South America), or plant-cutters; Menuridae (2. Australia), or lyrebirds; Atrichornithidae (2. Australia), or scrub-birds; Irenidae (14. Indo-Malayan area), or fairy bluebirds and leafbirds; Vangidae (11. Madagascar), or vangas; Bombycillidae (9. Holarctic and Central American), or waxwings; Dicaeidae (54. Indo-Australian), or flowerpeckers; Nectariniidae (104. Old World tropics), or sunbirds; Tersinidae (1. Neotropical), or swallow-tanager; Grallinidae (11. Australia), or magpie-larks and allies; and Callaeidae (3. New Zealand), or wattlebirds. Most of these are small families, of restricted distribution in the tropics, so that the lack of records is not surprising and may be due to insufficient collecting. The absence of flies on any of the Nectariniidae is, however, more difficult to account for in this manner.

Among the remaining 34 families, to be discussed presently, the following 21 have so few known hippoboscid records that most of them probably never are true breeding hosts: Rhinocryptidae, Formicariidae, Furnariidae, Pittidae, Cotingidae, Alaudidae, Pycnonotidae, Campephagidae, Prunellidae, Motacillidae, Ptilonorhynchidae, Artamidae, Certhiidae, Sittidae, Cracticidae, Zosteropidae, Vireonidae, Drepaniidae, Ploceidae, Dicruridae, and Paradisaeidae. This leaves only 13 families which on present evidence may be regarded as of prime importance for the effective survival of the hippoboscids of the passerines. It is too early, however, to eliminate definitely as possible true breeding hosts all the 37 families listed above.

(1) Rhinocryptidae (26. Neotropical), or tapaculos. A single record of *Ornithoctona fusciventris* on *Scytalopus* was probably based on a straggler.

(2) Formicariidae (221. Neotropical), or antbirds and their allies. Considering the number of species and their relative abundance, the fly records from these birds are very few, which may be due to insufficient collecting. *Ornithoctona fusciventris* was taken a few times from *Grallaria* and *Thamnophilus*. There is also one record of *Ornithoica vicina* from *Drymophila* and another of *Stilbometopa podopostyla* from *Chamaeza*.

(3) Furnariidae (259. Neotropical), or ovenbirds and woodhewers. *Ornithoctona erythrocephala* has been reported from *Magarornis; Ornithoctona fusciventris* from *Synallaxis* (as the type host of *Ornithomyia synallaxidis,* a synonym of *fusciventris*) and *Lepidocolaptes; Ornithoica vicina* from *Thripadectes* and *Xenoctistes; Ornithomyia remota* from *Cinclodes;* and *Ornithomyia* (*Pseudornithomyia*) *ambigua,* otherwise a specific parasite of Hi-

rundinidae, from *Xenops*. All these are clearly stray occurrences and, like the preceding family, the Furnariidae probably never serve as breeding hosts.

(4) Pittidae (23. Old World tropics), or pittas. Three common Oriental hippoboscids, *Ornithoica pusilla, Ornithoctona australasiae,* and *Ornitheza metallica,* have been taken as accidental strays on *Pitta* in the Indo-Malayan area.

(5) Tyrannidae (366. American), or tyrants. There are a fair number of records of *Ornithomyia fringillina* from *Sayornis* and *Tyrannus;* of *Ornithoica vicina* from *Pitangus, Pyrocephalus,* and *Tyrannus;* and of *Ornithoctona fusciventris* from *Colonia, Empidonax,* and *Muscisaxicola;* these birds are most probably true breeding hosts of the flies. Whether the isolated finds of *Ornithoctona oxycera* on *Myiodynastes* and of *Ornithomyia remota* on *Muscisaxicola* and *Agriornis* are more than accidental cannot be decided.

(6) Cotingidae (90. Neotropical), or cotingas. The very few known occurrences of *Ornithoica vicina* on *Pyroderus* and *Cephalopterus,* of *Ornithoctona erythrocephala* on *Platypsaris,* and of *Lynchia angustifrons* on *Pyroderus* are no doubt accidental.

(7) Alaudidae (75. Old World), or larks. I can find only five definite records of *Ornithomyia avicularia* and *O. fringillina* from *Galerida* in Europe, one of *Ornithomyia* sp. from *Alauda* in Europe, one of *Ornithoica turdi* from *Mirafra* in Africa, and one of *Pseudolynchia canariensis* from *Galerida* in Africa. It seems strange that these birds are not more often infested with the common bird-flies of the other song birds.

(8) Hirundinidae (75. Cosmopolitan), or swallows and martins. This family is by far the most interesting from our point of view. Structurally and ecologically, the swallows show some extreme specializations, which set them apart from all other Passeriformes and have produced by convergence a similarity to the swifts. Although retaining the ability to perch, which the swifts have largely lost, the swallows are truly aërial birds, spending most of their life aloft, as they catch their insect food on the wing and nest in lofty situations. In some genera the nests are unusually solid and lasting structures, to which the birds may return year after year. The sand martins (*Riparia*), however, burrow in the soil and then bring in some loose nest material on which the eggs are laid. Many species are gregarious, nesting in colonies or gathering for seasonal migrations. The plumage consists of fine, but stiff, closely appressed contour feathers, giving the body a smooth, sleek,

streamline appearance. It affords an ideal abode for louse-flies, particularly for species with reduced wings, which glide with ease under the feathers. The bill, moreover, is poorly built to catch rapidly moving, flat flies within the plumage. Mainly in response to the high speed and aërial habits of the hosts, the flies of the Hirundinidae have acquired several special adaptations similar to those of the swift flies, such as the extreme flattening of the body, the insertion of the head in a deep anterior notch of the thorax, and the strong, deeply bifid claws. So far as known, all the specific flies of swallows deposit the larvae in the nests, where the puparia overwinter when the birds leave for their migrations.

It should be noted that the European house martin, *Delichon urbica,* now habitually nests in buildings, in close vicinity to Man. It is occasionally observed nesting under the original, natural conditions on cliffs or on the roofs of caves. It might be instructive to determine whether its specific fly, *Stenepteryx hirundinis,* is as abundant in the natural as in the artificial nesting sites.

In most geographical areas, swallows harbor peculiar, specific hippoboscids: in the Palearctic Region, *Stenepteryx hirundinis* occurs on *Delichon* and *Ornithomyia biloba* on *Hirundo;* in southern Asia to Australia, *Ornithomyia comosa* on *Riparia* and *Petrochelidon;* in Africa, *Ornithomyia fur* (= *Ornithomyia roubaudi* Séguy, 1938) on *Hirundo, Cecropis,* and *Psalidoprocne,* and *Ornithomyia inocellata* on *Petrochelidon;* in tropical America, *Crataerina seguyi* on *Alopochelidon* and *Notiochelidon,* and *Ornithomyia* (*Pseudornithomyia*) *ambigua* on *Iridoprocne, Notiochelidon, Progne,* and *Stelgidopteryx.*

In Europe, there are a few trustworthy published stray records of *Crataerina pallida,* the specific parasite of the swift, *Apus apus,* on *Hirundo rustica* (Massonat, 1909, p. 327); of *Ornithomyia biloba* on *Delichon* and *Riparia;* and of *Stenepteryx hirundinis* on *Hirundo* and *Riparia* (Walsh, 1924*b*, in England). Most such records, however, must be disregarded as either faulty or unreliable. Moreover, it is as yet doubtful that these flies breed regularly on the abnormal hosts. "*Lynchia nipponica*" Kishida (in Esaki, 1932), described in Japan from *Delichon urbica dasypus,* is clearly a species of *Stenepteryx* and, I believe, not separable from *S. hirundinis.* I am unable to guess the identity of the same author's "*Brachypteromyia nakamurai,*" from *Hirundo rustica gutturalis,* presumably in Japan (or perhaps Formosa?); the host of this may have been erroneous.

Probably most early European records of *Ornithomyia avicu-*

laria and *O. fringillina* from *Hirundo rustica* and *Delichon urbica* were based on the failure to recognize *O. biloba* Dufour (= *O. tenella* Schiner). In England, however, where *O. biloba* is not known to occur, both *O. avicularia* and *O. fringillina* are reported from *Delichon* and *O. fringillina* also from *Hirundo.* There is one, rather dubious, stray record of *Ornithoica turdi* from *Delichon urbica* in Portugal (Braga, 1942). I am inclined to regard as either accidental or due to faulty observations a record of *Ornitheza metallica* from *Cheramoeca* in Australia, and two records of *Ornithoctona laticornis* (= *platycera*) from *Hirundo* and *Cecropis* in Africa, of which I saw the flies.

(9) Pycnonotidae (109. Old World tropics), or bulbuls. These birds have yielded thus far only a few stray records: one of *Ornitheza metallica* from *Pycnonotus* in Transvaal; one of *Ornithoctona australasiae* from *Pycnonotus* in Java; and one of *Ornithoica turdi* from *Andropadus* in Uganda.

(10) Campephagidae (72. Old World), or cuckoo shrikes. All known records from these birds are based on strays: *Ornithoica turdi* was taken on *Campephaga* in Africa; *Ornithoctona australasiae* on *Edolisoma* in Australia; and *Ornithoctona plicata* on *Pericrocotus* in the Far East. I have seen *Ornithoica stipituri* from *Coracina* in New Guinea.

(11) Muscicapidae (1460. Cosmopolitan). I follow Mayr and Amadon in including in the Muscicapidae the following subfamilies, which other ornithologists prefer to rank as families: Timaliinae, Sylviinae, Turdinae, Miminae, Troglodytinae, and Cinclinae. A further subdivision of the family seems needless from my point of view, as it would add nothing of value to an understanding of the relations between the hosts and the flies. The family contains a variety of usually small, insectivorous song birds. Many of them are the usual breeding hosts of the more common louse-flies, none of which, however, exhibit any marked host specificity. In Europe, *Ornithomyia fringillina* and *O. avicularia* occur on *Oenanthe, Phoenicurus, Phylloscopus, Regulus, Sylvia, Turdus,* and *Erithacus; O. fringillina* also on *Luscinia, Hippolais, Cinclus, Acrocephalus,* and *Muscicapa; O. avicularia* also on *Troglodytes;* and *Ornithoica turdi* on *Monticola* and *Muscicapa.* In North America, both *Ornithomyia fringillina* and *Ornithoica vicina* are common parasites of *Dendroica, Dumetella, Hylocichla, Mniotilta, Wilsonia, Turdus, Seiurus,* and *Troglodytes;* while *O. fringillina* is furthermore known from *Compsothlypis* (or *Parula*), *Geothlypis, Helmitheros, Thryomanes, Icteria, Toxostoma, Thryothorus, Vermivora, Myadestes, Setophaga,*

and *Sialia,* and *O. vicina* from *Cinclus, Corthylio, Chamaea,* and *Mimus;* in the same area, *Ornithoctona fusciventris* occurs fairly often on *Wilsonia, Dendroica,* and *Setophaga,* and probably uses these birds as breeding hosts. In tropical America, *Ornithoctona fusciventris* is found on *Cinnycerthia, Platycichla, Turdus, Seiurus, Mniotilta,* and *Dendroica;* and *Ornithoica vicina* on *Turdus;* in addition, *Ornithomyia remota* seems to be a normal parasite of *Nesocichla* (in Tristan da Cunha), *Turdus,* and *Mimus.* In Africa, *Ornithoctona laticornis* (= *platycera*) occurs regularly on *Myrmecocichla, Pratincola, Turdus, Batis, Cossypha, Tchitrea, Dioptrornis, Bessorornis, Sylvietta,* and *Seicercus; Ornithoica turdi* is known from *Dioptrornis, Alethe, Alseonax, Cossypha,* and *Batis,* and *Ornitheza metallica* from *Turdus, Melocichla,* and *Oenanthe.* In the Indo-Malayan and Pacific areas, as well as in the Mascarenes, *Ornithoctona plicata* occurs on *Cossypha, Ornithoica pusilla* on *Myiagra* and *Piezorhynchus,* and *Ornitheza metallica* on *Muscicapa* and *Myiagra. Ornithomyia fringillina* was taken on *Copsychus* in China; *O. avicularia* on *Elachura* in Ceylon and on *Cinclosoma* in Australia; and *Pseudolynchia canariensis* on *Cinclus* in southern Asia.

The following occurrences of other species of flies on Muscicapidae are probably all accidental: *Lynchia samoana* on *Myiagra* and *Turdus* in the Pacific; *Ornithoica stipituri* on *Stipiturus* in Australia; *Lynchia hirsuta* on *Toxostoma* in North America; *Microlynchia pusilla* on *Mimus* in North America; *Pseudolynchia brunnea* and *Lynchia angustifrons* on *Hylocichla* in North America; *Ornithoctona oxycera* on *Dendroica* and *Turdus* in tropical America; and *Ornithoctona* (*Ornithopertha*) *nitens* on *Turdus* in South America.

(12) Prunellidae (12. Palearctic), or hedge sparrows. Both *Ornithomyia fringillina* and *O. avicularia* have been reported from *Prunella* in Europe, perhaps as strays.

(13) Motacillidae (48. Cosmopolitan), or wagtails and pipits. The surprisingly few records from these birds are possibly all based on stragglers. *Ornithomyia fringillina* and *O. avicularia* have both been taken on *Motacilla* and *Anthus* in Europe; and a species of *Ornithomyia* also on *Anthus* in the Philippines.

(14) Laniidae (67. Old World and Nearctic), or shrikes. The few known records are all of common parasites of song birds: *Ornithomyia avicularia* and *O. fringillina* on *Lanius* in Europe and (*fringillina* only) in North America; *Ornithoica turdi* on *Tchagra, Dryoscopus, Laniarius,* and *Malaconotus* in Africa, and on *Lanius*

in Japan; *Ornithoctona laticornis* (= *platycera*) on *Dryoscopus, Lanius, Antichromus, Chlorophoneus,* and *Tchagra* in Africa; and *Ornitheza metallica* on *Malaconotus* in Africa. The scarcity of fly records from shrikes may be due to insufficient collecting, and these birds may well be normal breeding hosts of some of the flies here mentioned.

(15) Prionopidae (14. Africa and Borneo), or helmet shrikes. The only record is that of a stray *Ornithoica turdi* from *Prionops* in Uganda.

(16) Artamidae (10. Indo-Malayan and Australian), or wood swallows. There are thus far only two records of *Ornithoctona plicata* from *Artamus* and *Artamides* in the Pacific area, both possibly based on stragglers.

(17) Certhiidae (6. Old World and Nearctic), or creepers. I know of only one record of *Ornithomyia fringillina* from *Certhia familiaris* in Europe.

(18) Sittidae (29. Old World, except Africa, and Nearctic), or nuthatches. There are a few, probably all stray, records of *Ornithomyia fringillina* in Europe and North America, of *Ornithoica vicina* in North America, and of *Ornithoctona plicata* in the Philippines, all from *Sitta.*

(19) Paridae (64. Cosmopolitan), or titmice. *Ornithomyia avicularia* and *O. fringillina* have been taken on *Parus* in Europe; and *O. fringillina* and *Ornithoica vicina* on *Penthestes* and *Baeolophus* in North America. Probably titmice are breeding hosts of these flies, along with the more usually infested song birds.

(20) Meliphagidae (160. Indo-Malayan, Australian and African), or honeyeaters. The few known records are of *Ornithomyia avicularia* from *Creadion* and *Anthochaera* in Australia; of *Ornitheza metallica* from *Meliphaga* in Tasmania; and of *Ornithoica pusilla* from *Philemon* in Australia. There is a possibility that, when better investigated, this family will be recognized as containing important breeding hosts.

(21) Zosteropidae (80. Old World tropics), or white-eyes. There is a single record of *Ornithoctona laticornis* (= *platycera*) from *Zosterops* in Africa, probably based on a stray fly.

(22) Vireonidae (41. American), or vireos. I know only one record of *Ornithoctona fusciventris* from *Vireo* in North America, possibly of a stray.

(23) Drepaniidae (22. Hawaiian Islands), or Hawaiian honeycreepers. These peculiar birds have no special fly, so far as known. There are two records only of *Ornithoica pusilla* from *Himatione*

and *Vestiaria.* The fly is a common parasite of a variety of birds throughout the Indo-Malayan and Pacific areas and most probably a recent introduction into the Hawaiian Islands, where the few known Hippoboscidae are probably all adventitious. The Hawaiian bird fauna consists nowadays mostly of species introduced by Man during the past two centuries.

(24) Thraupidae (474. American), or tanagers, wood warblers, honeycreepers, etc. It is surprising that hippoboscids have been so little collected on this large family of rather conspicuous birds. Most of the records are for the tropical areas: *Ornithoctona fusciventris* from *Calospiza, Dubusia, Piranga, Poecilothraupis,* and *Tachyphorus; Ornithoctona oxycera* from *Thraupis;* and *Ornithoica vicina* from *Ramphocelus.* In North America, there seem to be only four records: two of *Ornithomyia fringillina* on *Piranga* and two of *Ornithoctona fusciventris* on *Conirostrum* and *Piranga.* The Thraupidae should be searched more carefully for parasitic flies.

(25) Fringillidae (293. Cosmopolitan, except New Guinea and Australia), or finches and allies. Birds of this family are greatly favored by a few species of louse-flies and, together with the Muscicapidae, are their main breeding hosts. In Europe, *Ornithomyia fringillina* is found on *Chloris, Emberiza,* and *Fringilla; O. avicularia* on *Carduelis* and *Fringilla;* an *Ornithomyia* of one or the other of these species on *Calcarius* and *Loxia;* and *Ornitheza metallica* on *Montifringilla, Carduelis* and *Emberiza.* In North America, *Ornithomyia fringillina* is commonly taken on *Ammodramus, Carpodacus, Hedymeles, Hesperiphona, Junco, Loxia, Melospiza, Passerculus, Passerella, Pipilo, Plectrophenax, Pooecetes, Richmondena, Spizella,* and *Zonotrichia; Ornithoica vicina* on *Ammodramus, Carpodacus, Hedymeles, Junco, Melospiza, Passerculus, Passerella, Pipilo, Pooecetes, Richmondena, Spizella,* and *Zonotrichia;* there are a few records of *Microlynchia pusilla* from *Arremonops, Pipilo,* and *Richmondena,* but what significance they have is as yet unclear. *Ornithoctona fusciventris* has been taken in North America on *Hedymeles,* and in the Neotropics on *Atlatepetes, Pselliophorus,* and *Zonotrichia.* In South America, *Ornithomyia remota* lives on *Zonotrichia, Diuca* and (in Tristan da Cunha) on *Nesospiza.* The single record of *Lynchia angustifrons* from a South American *Pitylus* may have been due to faulty observation. In Africa, *Ornithoctona laticornis* (= *platycera*) is recorded from *Serinus, Poliospiza,* and *Spinus;* and *Ornithoica turdi* from *Serinus.* There is evidently nothing distinctive about the hippo-

boscid fauna of the Fringillidae, which is much the same as that of the Muscicapidae and Corvidae.

(26) Icteridae (88. American), or troupials and American blackbirds. These birds are frequent breeding hosts of the common flies of song birds. Most of the known records are from North America: *Ornithomyia fringillina* on *Agelaius, Dolichonyx, Euphagus, Icterus, Molothrus,* and *Quiscalus; Ornithoica vicina* on *Agelaius, Euphagus, Molothrus,* and *Quiscalus;* and a single, no doubt stray, record of *Microlynchia pusilla* from *Sturnella.* There is one capture of *Ornithoctona erythrocephala* on *Holoquiscalis* in the Antilles; also one of *Ornithoctona fusciventris* and another of *Ornithomyia remota* on *Sturnella* in South America. The bird-flies of the Central and South American Icteridae need to be collected more intensively.

(27) Ploceidae (263. Old World), or sparrows, weaverbirds, widow-birds and allies. Although fairly numerous in species and often abundant, these birds seem to attract few hippoboscids. In Europe, *Ornithomyia fringillina* has been taken a few times on *Passer domesticus;* also in North America, where the domestic sparrow is a recent introduction by Man. There is one European record of *Crataerina pallida,* of swifts, from the same bird. In Africa *Ornithoctona laticornis* (= *platycera*) occurs frequently on *Lagonosticta, Ploceus, Coliuspasser, Euplectes,* and *Coccopygia; Ornithoica turdi* on *Passer griseus;* and *Ornitheza metallica* on *Quelea.* The American *Ornithoica vicina* is sometimes found on the introduced *Passer domesticus* in Hawaii (Alicata, *et al.,* 1948) and in North America. With the exception of *Ornithoctona laticornis,* the flies mentioned above are probably accidental strays.

(28) Sturnidae (103. Old World), or starlings and tick-birds. In Europe, hippoboscids seem to occur on these birds only as accidental strays, *Ornithomyia avicularia* and *O. fringillina* being rarely taken on *Sturnus.* In India, there is one record of *Pseudolynchia canariensis* from *Temenuchus,* one of *Ornitheza metallica* from *Pastor roseus* (Eichler, 1939*b*, p. 223), and one of an unidentified *Ornithoica* from *Acridotheres* (Ansari, 1949, p. 216). In Africa, *Ornithoctona laticornis* (= *platycera*) has been recorded from *Cinnamopterus, Cinnyricinclus,* and *Creatophora; Ornitheza metallica* from *Lamprocolius, Onychognathus,* and *Stilbopsar;* and *Ornithoica turdi* from *Lamprotornis* and *Stilbopsar.* In the Pacific area, both *Ornitheza metallica* and *Ornithoica pusilla* have been taken on *Aplonis.* In North America, *Ornithomyia fringillina* occurs occasionally on the introduced feral European starling,

Sturnus vulgaris, and Oriental crested mynah, *Acridotheres cristatellus.* Carpentier (1952) reports finding at Liege, Belgium, 4 swift flies, *Crataerina pallida,* on a dead juvenile *Sturnus vulgaris,* a most unusual occurrence.

(29) Oriolidae (34. Old World), or orioles. *Ornithomyia* (? *avicularia*) in Europe, *Ornithoica turdi* and *Ornithoctona laticornis* (= *platycera*) in Africa, *Ornithoctona australasiae, O. plicata* and *Ornitheza metallica* in the Pacific area, have all been recorded from *Oriolus;* but whether these birds serve as regular breeding hosts for any of the flies is doubtful.

(30) Dicruridae (20. Old World), or drongos. I find only three hippoboscid records for these birds: *Ornithoctona laticornis* (= *platycera*) in Africa, *Ornithoctona soror* in Borneo, and *Ornithoica pusilla* in the Pacific area, all from *Dicrurus.* Some of these may have been stray occurrences.

(31) Corvidae (100. Cosmopolitan), or crows, jays and magpies. To judge from the fairly numerous fly records, these birds seem to be, at least in some cases, true breeding hosts. In Europe, both *Ornithomyia avicularia* and *O. fringillina* are recorded from *Corvus, Garrulus,* and *Pica; O. avicularia* also from *Coloeus;* and *Ornitheza metallica* from *Garrulus* and *Pyrrhocorax.* In North America, both *Ornithomyia fringillina* and *Ornithoica vicina* are found on *Aphelocoma, Corvus, Cyanocitta,* and *Perisoreus;* and *O. vicina* also on *Pica.* In tropical America, *Ornithoctona erythrocephala* was found on *Corvus* and *Cyanolyca; O. fusciventris* on *Xanthoura; Ornithoica vicina* on *Cyanocorax* and *Uroleuca;* and *Lynchia angustifrons* (no doubt a stray) on *Cyanocorax.* In Africa, *Ornithoica turdi, Ornitheza metallica,* and *Pseudolynchia rufipes* are all reported from *Corvus.* In the Indo-Malayan area, *Ornitheza metallica* and *Ornithoctona plicata* occur on *Corvus,* and *Ornithoica pusilla* and *Ornithomyia avicularia* on *Kitta;* the type host of *Lynchia tuberculata* Ferris (1927c), of the Philippines, is a species of *Corvus. Ornithomyia avicularia* has also been taken on *Corvus* in Australia.

(32) Cracticidae (11. New Guinea, Australia), or bell magpies. I have seen specimens of *Ornithomyia avicularia* taken in Australia on two species of *Strepera.* Future collecting will have to decide whether or not these were stray occurrences.

(33) Ptilonorhynchidae (17. New Guinea, Australia), or bowerbirds. In Australia, *Ornithoica pusilla* was taken on *Aeluroedus,* and *Ornithomyia perfuga* on *Sericulus.* Again the records are too few to be of much significance.

(34) Paradisaeidae (43. New Guinea, Australia), or birds of paradise. The only known record is of a species of *Ornithoica* from *Diphylodes magnificus,* in New Guinea, possibly based on a stray or contamination. Speiser (1900, p. 557) determined the fly as *O. beccariina.* The true *O. beccariina* is, however, a synonym of *O. confluenta,* hence a specific parasite of wading birds, so that Speiser's identification may have been erroneous.

II. Mammals. I have adopted the limits, names and sequences of the orders, families and genera of G. L. Simpson (1945). Unfortunately no single up-to-date work gives the number of the Recent or living species known in each order and family or their present distribution and ecology. Information on such matters was obtained from a variety of sources, particularly from G. M. Allen (1939) for the African fauna and from Ellerman and Morrison-Scott (1951) for that of Europe and Asia.

Of the 18 Recent orders recognized by Simpson, 13 contain no known breeding hosts of louse-flies: Monotremata, Insectivora, Dermoptera, Chiroptera, Edentata, Pholidota, Lagomorpha, Rodentia, Cetacea, Tubulidentata, Proboscidea, Hyracoidea and Sirenia. Even stray flies are very rare on these, the most trustworthy of such reports being mentioned elsewhere in this paper.

The absence of Hippoboscidae from the Chiroptera, or bats, must be stressed, since these mammals are the only known breeding hosts of the other two families of pupiparous parasitic flies, the Nycteribiidae and the Streblidae.[21] The few published reports to the contrary should be disregarded as unreliable. A case in point is *Lipoptena pteropi* Denny (1843), which the author claimed to have collected himself from an East Indian fruit-bat; unfortunately the description is unrecognizable and the specimen appears to be lost, so that it may never be possible to determine its true host (J. Bequaert, 1942*a,* p. 210). Although many fruit-bats have been examined for ectoparasites in the East Indies and elsewhere, they have never yielded a trustworthy record of a hippoboscid.

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[21] Reported occurrences of Streblidae on mammals other than bats or on birds may safely be dismissed as due to faulty observation, *post mortem* or other contaminations, or mislabelling of specimens. The following records belong in this category: Macquart's (1855) *Strebla avium,* which he stated came from doves and parrots in Santo Domingo, and which remains unrecognized to this day (most probably based on one of the common West Indian species of *Trichobius*); and Kessel's (1924, *Parasitology,* **16,** p. 409) *Euctenodes mirabilis* from an opossum, *Glironia venusta,* in Bolivia.

The present discussion deals only with wild hosts in nature. The origin and present-day host relations of the louse-flies of domesticated mammals are a special problem, to be considered later. The Hippoboscidae sometimes attacking Man, who is never more than an accidental and temporary host, will also be treated separately.

1. **Order Marsupialia,** or marsupials, nowadays restricted to the New World and to the Australian area (New Guinea, the Bismarck Archipelago, the Solomons, the Aru and Kei Islands, Australia and Tasmania). Of the 8 Recent families recognized by Simpson (1945), only the Macropodidae of the Australian area are known to harbor flies, all of the subfamily Ortholfersiinae, the so-called wallaby-flies. Moreover, the flies occur only on members of the subfamily Macropodinae, comprising the kangaroos and wallabies. Formerly these were all included in the one genus *Macropus;* at present they are grouped in 10 genera, with 29 species (Tate, 1948, *Bull. Amer. Mus. Nat. Hist.,* **91,** pp. 278–336). They are terrestrial, strictly vegetarian animals, which use the greatly lengthened hind limbs and tail to progress on the ground by a series of leaps. The skin is covered with a rather thick fur. The female carries the young for some time after birth in a ventral pouch. The larger species congregate in droves, but the others associate in small parties or in pairs.

The taxonomy of the Ortholfersiinae is at present greatly confused and very little work has been done either on the details of their host relations or on other points of their life history. While there is no reason to doubt that they are pupiparous, larviposition has not actually been observed, nor the puparium described. At present, flies are definitely recorded only from two genera of wallabies, or medium-sized and smaller Macropodinae, *Protemnodon* and *Thylogale.*

The wallaby-flies I have seen belong to three or possibly four species referable to two genera. Four specific names have been proposed for them: *Feronia macleayi* Leach (1817, p. 12), *Ortholfersia phaneroneura* Speiser (1902*b*, p. 153), *Hippobosca tasmanica* Wesché (1903, p. 385), and *Ortholfersia raveni* Ferris (1924*b*, p. 4). Whether these refer to two or to three species cannot yet be decided. So much is certain that all four descriptions were based on species of the genus *Ortholfersia* Speiser (1902*b*, p. 152), originally monotypic for *Ortholfersia phaneroneura.* This genus has a characteristic wing venation, with the full complement of longitudinal veins, the third longitudinal being present (Fig. 14B; see also Ferris, 1924*b*, p. 5, fig. 4, wing of *O. raveni*). Species of *Ortholfersia* are now definitely known from two subspecies of *Protemnodon rufogrisea* (= *Macropus ruficollis*), in Tasmania and New South Wales, and from *Protemnodon parryi*, in New South Wales.

One species of wallaby-flies differs from the foregoing in that the wing has only five longitudinal veins, the third longitudinal being absent (Fig. 14C; see also Ferris, 1924*b*, p. 3, fig. 2A, wing of his supposed *O. tasmanica*). This peculiarity of the venation was first noticed by Ferris (1924*b*) in a species which he retained in *Ortholfersia* and referred to *Ortholfersia tasmanica* Wesché. A study of Wesché's type of *Hippobosca tasmanica*, at the British Museum, shows, however, that it has the complete venation of *Ortholfersia*. Ferris' supposed *O. tasmanica* is distinct also from the other species of wallaby-flies listed above. I now propose to erect the new genus **Austrolfersia** for the wallaby-flies with only five longitudinal veins. The type is **Austrolfersia ferrisi**, new name for *Ortholfersia tasmanica* Ferris, 1924, not *Hippobosca tasmanica* Wesché, 1903. Ferris described the species in detail. I have examined some of his material, as well as other specimens. *Austrolfersia ferrisi* is known so far only from *Thylogale stigmatica*, in Queensland.

As Speiser (1904*d*, p. 390) pointed out, the supposed occurrence of a species of *Ornithomyia* on wallabies, reported by Austen (1903, p. 261; 1906, p. 64), was based on erroneous information.

Seddon (1951, p. 111) states that, when wallabies are killed, their louse-flies frequently attack dogs. It would be of much interest to know how long the flies remain on dogs and whether they actually bite them.

2. **Order Primates**, or apes, monkeys, lemurs, tarsiers and other related, more or less monkey-like animals; includes Man also. It is cosmopolitan, mainly in the tropics, and is absent from Australia (except for Man). Only two of the 11 Recent families recognized by Simpson (1945) are known to harbor hippoboscids: the Lemuridae, or lemurs (6 genera, with 16 species, according to G. M. Allen, 1939); and the Indriidae, or woolly lemurs and sifakas (3 genera, with 4 species). Both families are restricted to Madagascar and the Comoros. The only lemur fly known is the strictly specific *Allobosca crassipes*, the only species of the genus and sole representative of the subfamily Alloboscinae. Although rarely collected, it is probably by no means rare on several genera and species

of hosts. There are published records in the Lemuridae from *Lepilemur mustelinus* (one of the type hosts; Speiser, 1899*a*) and *Lemur* sp. (probably *Lemur rubriventer* = *L. rufipes;* Speiser, 1908*b*), and in the Indriidae from *Propithecus diadema* (one of the type hosts; Speiser, 1899*a*) and *Propithecus diadema edwardsi* (Ferris and Cole, 1922).

In 1948, while a member of a United States Naval Medical Science Group, Mr. H. Hoogstraal had the opportunity to collect ectoparasites from 22 fresh specimens of lemurs at Mananterna, Post Bemangidy, in the Fort Dauphin District of Madagascar. According to information kindly supplied by him, *Allobosca* was found on all 6 *Lemur macaco collaris* (Fam. Lemuridae) and on the one *Avahi l. laniger* (Fam. Indriidae) examined. In addition, 4 *Lemur catta* (Lemuridae), 2 *Microcebus m. murinus* (Lemuridae), 4 *Microcebus murinus rufus,* 3 *Cheirogaleus m. medius* (Lemuridae), and 2 *Propithecus v. verreauxi* (Indriidae) carried no flies.

Little is known as yet of the life-history of *A. crassipes.* It is assumed that it is pupiparous, but the larviposition and puparium have not been observed. All known specimens of both sexes are subapterous, with the wings reduced to short, broad flaps with a few heavy veins (see Ferris and Cole, 1922, p. 191, fig. 7A; and my Fig. 12H). I am not certain, however, that the wings may not be more complete or even functional when the fly emerges from the puparium, before it settles on the host (as in *Lipoptena*). There seem to be jagged edges of membrane along the heavy vein bordering the hind margin of some of the wings I examined.

3. **Order Carnivora** (including Pinnipedia), or felines, canines, bears and their relatives. This is a large, cosmopolitan group of carnivorous and predatory, mainly terrestrial, rarely aquatic animals, of medium to fairly large size, the body usually covered with thick, dense fur. Some live in pairs or small families, others gather in packs. Of the 11 families accepted by Simpson (1945), three are known to contain wild hosts of *Hippobosca longipennis* (= *H. canina; H. capensis*), the dog-fly so abundant on domestic dogs in the Near and Far East and India. On wild hosts, the fly is known mainly from eastern Africa (Egypt, Kenya and Tanganyika), with reliable records from Canidae: jackals, *Canis* (*Thos*) *adustus, C.* (*Thos*) *aureus, C.* (*Thos*) *mesomelas,* and Egyptian fox, *Vulpes vulpes aegyptiaca;* Viverridae: civets, *Civettictis civetta schwarzi* (= *Viverra civetta orientalis*); Hyaenidae: spotted hyena, *Crocuta crocuta fisi* and *C. c. germinans,* and striped hyena, *Hyaena hyaena dubbah* (= *H. h. schillingsi*); and Felidae: cheetah, *Acinonyx juba-*

tus raineyi, serval, *Felis* (*Leptailurus*) *serval hindei,* leopard, *Panthera pardus pardus* (=*P. p. suahelica*), and lion, *Panthera* (*Leo*) *leo massaica.* Some of these animals are true breeding hosts; Matthews (1939, p. 52) found the flies in Tanganyika plentifully on spotted hyenas and lions, in lesser numbers on cheetahs. Possibly the dog-fly only strays occasionally to some of the other wild Carnivora; but the matter calls for further investigation.

4. **The Order Perissodactyla** contains the horses, tapirs, and rhinoceroses. In the Recent fauna, it is a relatively small cosmopolitan group of large to very large, terrestrial, vegetarian animals. Many are almost devoid of hair; in others the fur is mostly short and coarse, except over certain long-haired areas of the body. Two of the 3 Recent families, the Tapiridae and the Rhinocerotidae have no louse-flies. In the Equidae, three species of *Hippobosca* occur in certain parts of the World on domestic equines (see below), but are not known from any wild member of the family. There is, however, one record of *Echestypus paradoxus,* normally a ked-fly of antelopes, from a South African zebra, *Equus* (*Hippotigris*) *burchellii antiquorum,* no doubt an accidental stray.

5. **The Order Artiodactyla** is very extensive and cosmopolitan. In the Recent fauna, it includes three suborders: Suiformes, or pigs, wart-hogs, pecaris, and hippopotamus; Tylopoda, or llamas and camels; and Ruminantia, or chevrotains, deer, giraffes, cattle, antelopes, sheep, goats, chamois and their relatives. They are all vegetarian, from fairly small to very large, usually terrestrial, rarely semi-aquatic, with fur of many different types. The order, more abundant nowadays in Africa than elsewhere, contains more true hosts of Hippoboscidae and harbors more species of these flies than the combined other four orders of mammals here discussed. All Melophaginae (with 22 species in 4 genera) are strictly parasitic of Artiodactyla (except for strays); and of the 8 species of Hippoboscinae, 6 occur regularly on members of this group.[22]

No Suiformes are normal hosts of louse-flies. In the family Suidae, or pigs and wart-hogs, there is an unconfirmed statement by R. Blanchard (1890, p. 494) that *Hippobosca equina,* a fly of equines and cattle, was found on domestic pig. In the Tayassuidae, or pecaris, the deer-ked, *Lipoptena mazamae,* was taken on one occasion in Texas from a pecari, *Tayassu angulatus,* presumably an accidental occurrence.

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[22] In the account of the Artiodactyla, the numerals following the generic names indicate the species now generally regarded as valid.

The Tylopoda comprise the one family Camelidae, with the genera *Lama,* the llamas and their relatives of South America, and *Camelus* of the Old World. *Hippobosca camelina* (= *dromedarina*) is the usual specific parasite of the two domesticated species of *Camelus, C. dromedarius,* the one-humped dromedary, and *C. bactrianus,* the two-humped camel; but it has not been taken on the few surviving wild *C. bactrianus* in Central Asia. I can find no reliable information in support of the claim, made in some textbooks, that the South American domesticated alpaca, *Lama glama pacos,* is an occasional host of the sheep-ked, *Melophagus ovinus.*

The many and varied Ruminantia call for more detailed treatment. The small family Tragulidae, or chevrotains, placed by Simpson (1945) in a special ''Infraorder Tragulina,'' comprises two genera: *Hyemoschus* (formerly included in *Dorcatherium*), of Africa, which has no known fly; and *Tragulus,* of the Indo-Malayan area, with 4 species, of one which, *T. javanicus* (= *T. kanchil*), is the specific host of *Lipoptena gracilis.*

The remaining ruminants, or Simpson's (1945) ''Infraorder Pecora,'' comprise four Recent families: Cervidae, Giraffidae, Antilocapridae, and Bovidae. Hippoboscids, of the subfamilies Hippoboscinae and Melophaginae, have been reported from all four; but two only, Cervidae and Bovidae, are definitely known to contain true breeding hosts.

The Cervidae comprise the deer, musk-deer, European elk or American moose, brockets, muntjaks, and their relatives. In the Recent fauna the family occurs in Europe, Asia, northwestern Africa, the Malay Archipelago, the Philippines and most of continental America. The prevalence of louse-flies on these animals is remarkable, since 9 of the 17 Recent genera recognized by Simpson are known to harbor them. They have not been found with certainty to breed on *Elaphodus* (1), *Elaphurus* (1), *Dama* (2), *Rangifer* (1), and *Hydropotes* (1), in the Old World, and on *Hippocamelus* (1), *Blastocerus* (1), and *Pudu* (1), in America. These animals should all be searched carefully for louse-flies. The remaining 9 genera are *Moschus* (1), *Muntiacus* (5), *Axis* (2), and *Capreolus* (1), in the Old World; *Odocoileus* (2), *Mazama* (11), and *Ozotoceros* (1. Perhaps not separable from *Blastocerus*), in South America; and *Cervus* (7 in the Old, 1 in the New World) and *Alces* (or *Alce;* 1 in both the Old and New World). It is worthy of note that the flies known to breed on Cervidae all belong to two genera of the subfamily Melophaginae, *Lipoptena* and *Neolipoptena. Lipoptena cervi* is common in Europe and Asia on the roebuck, *Capreolus capreolus,* the red deer, *Cervus elaphus,* the Far-Eastern deer, *Cervus nippon,* and the European elk, *Alces alces.* It was introduced accidentally in the northeastern United States, where it is now established on the Virginia deer, *Odocoileus virginianus,* with one record from the wapiti or American elk, *Cervus canadensis,* which is perhaps a subspecies only of the Old World *Cervus elaphus.* I regard its occurrence in Europe on the fallow deer, *Dama dama,* as extremely doubtful. *L. pauciseta* is found on the muntjak, *Muntiacus muntjak,* in Indo-China, Siam, southern China and Sumatra. *L. rusaecola* is specific of the sambar deer, *Cervus* (*Rusa*) *unicolor,* in the Philippines; Dr. G. M. Kohls recently sent me some specimens collected from the ''sacred deer of Nara,'' in Japan, evidently a case of introduction with the host similar to that of *L. cervi* in North America.[23] Another species, *L. efovea,* peculiar to Ceylon, was taken on a local race of the muntjak, *M. m. malabaricus,* as well as on the chital or axis deer, *Axis axis.* Pallas (1777) described *L. moschi* (as *Hippobosca moschi*) from the Siberian musk-deer, *Moschus moschiferus,* and it is unfortunate that the species was not collected again for over 150 years. In the New World, *L. depressa* and *Neolipoptena ferrisi* are common parasites of the mule deer, *Odocoileus h. hemionus,* the black-tailed or coast deer, *O. h. columbianus,* and the western white-tailed deer, *Odocoileus virginianus leucurus,* in the western United States and western Canada. *L. depressa* was also taken once on the wapiti, *Cervus canadensis,* perhaps accidentally. The other common American species, *L. mazamae,* extends from the southeastern United States to northern Argentina, occurring on at least 6 races of the white-tailed deer, *Odocoileus virginianus,* as well as on several species of *Mazama,* or brockets (*M. americana, M. tema,* and *M. simplicicornis*). I have recently received from Dr. L. R. Guimarães specimens of an undescribed *Lipoptena* collected on the pampas deer, *Ozotoceros bezoarticus,* in Matto Grosso, Brazil. Other types of flies stray very rarely to deer. Johnsen (1948, p. 280) reports a *Hippobosca equina* from deer (*Capreolus capreolus*) in Denmark; and Edwards (1919, p. 55) mentions *Ornithoctona* sp. from a muntjak, *Muntiacus muntjak montanus,* in Sumatra, evidently fortuitous occurrences.

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[23] I wish to use this opportunity to correct an oversight in my Monograph of the Melophaginae (1942*a,* p. 112). I should have mentioned that Ferris (1930*b,* p. 547, figs. 6 and 7*a*) first described and figured the ked of the sambar deer, without naming it, from Mt. Maquiling, Luzon, without host.

The family Giraffidae, nowadays restricted to Africa, comprises the two Recent genera, *Giraffa,* the giraffes (2 species), and *Okapia,* the okapi (1 species). *Giraffa camelopardalis* is the type host of *Hippobosca camelopardalis* Roubaud (1925), based on one lot of specimens from Tanganyika, a fly which I regard as not separable from the more widespread *H. rufipes.* It is even doubtful that the giraffe was more than an accidental host.

The family Antilocapridae is strictly North American, with a single Recent genus and species, *Antilocapra americana,* the pronghorn or American antelope. There are now two records of *Neolipoptena ferrisi* from this animal (1 winged ♀ in one case; 1 ♀ and 1 ♂, both deälated and actually feeding in the other); further observations must decide whether or not they were due to temporary straying.

The family Bovidae is by far the most interesting group of mammalian louse-fly hosts and it will be useful for our purpose to divide it further. Simpson (1945) recognizes 5 subfamilies only, all of which contain breeding hosts of hippoboscids: the Bovinae, Hippotraginae, Cephalophinae, Antilopinae, and Caprinae. This is considerably less than the 16 subfamilies which I used in my Monograph of Melophaginae (1942*a,* pp. 33–35), where I followed Lydekker's Catalogue. Simpson includes the Tragelaphinae in the Bovinae; the Reduncinae, Alcelaphinae, and Oryginae in the Hippotraginae; the Neotraginae, Aepycerotinae, Madoquinae, and Oreotraginae in the Antilopinae; and the Rupicaprinae, Ovibovinae, Pantholopinae, and Saiginae in the Caprinae. He retains only the Cephalophinae with Lydekker's limits.

a. The Bovinae of Simpson comprise not only the wild and domestic cattle, buffaloes, and bisons, but also some of the larger antelopes, such as the kudus, harnessed antelopes, nilgai and their relatives. In the Recent fauna it is mainly an Old World group, represented in America only by the genus *Bison,* which, however, occurs also in Europe. There is no record of a hippoboscid living normally on any wild member of the cattle group strictly speaking, namely the genera *Bubalus* (1) or Asiatic water buffaloes, *Anoa* (1) or anoas, *Bos* (3) or cattle and yaks, *Bibos* (3) or bantengs and gaurs, *Syncerus* (2) or African buffaloes, and *Bison* (2) or American buffaloes and European wisents. Two species of *Hippobosca* infest domestic cattle in certain parts of the world, and these animals are sometimes accidental hosts of other flies also (see below). *Hippobosca equina* and *Melophagus ovinus* have been taken on the European aurochs or wisent, *Bison bonasus,* in Poland (Wrublewski, 1912, p. 384), presumably as accidental strays. Among the antelope-like genera, *Tetracerus* (1), the four-horned antelope, and *Boselephas* (1), the nilgai, both Asiatic, have no recorded fly in nature; I reported the accidental occurrence of the deer-ked, *Lipoptena cervi,* on a nilgau in an American zoological park (1942*a,* p. 72). The two remaining genera are African: *Strepsiceros* (5; includes *Tragelaphus,* according to Simpson) and *Taurotragus* (2). The most common African ked, *Echestypus paradoxus* (in Melophaginae), uses 4 species of *Strepsiceros* as regular breeding hosts: *S. strepsiceros,* the greater kudu, *S. imberbis,* the lesser kudu, *S.* (*Tragelaphus*) *angasi,* the nyala, and *S.* (*Tragelaphus*) *scriptus,* the bushbuck. This ked was also taken on one occasion from *Taurotragus oryx,* the eland, in Nyasaland. In addition, there are isolated records of *Echestypus sepiaceus* from *Strepsiceros strepsiceros* in Nyasaland and from *S.* (*T.*) *scriptus* in Uganda; and one reported find of *Lipoptena hopkinsi* on *S.* (*T.*) *scriptus* in the eastern Belgian Congo. *Hippobosca rufipes,* a fly commonly found on domestic equines in South Africa, was taken by two different collectors in Tanganyika on *Taurotragus oryx,* which may be one of its few known wild breeding hosts. There is one record of *Hippobosca fulva* from *Strepsiceros* (*T.*) *scriptus.*

b. The Cephalophinae, or duikers, are small antelopes, restricted to Africa. Of the 3 genera, *Philantomba* (1) has no known fly. In *Sylvicapra* (2), *S. grimmia* is one of the regular hosts of *Echestypus paradoxus.* Three of the 16 species of *Cephalophus* harbor flies: *C. caerulus* and *C. rufilatus* are usual hosts of *Echestypus sepiaceus,* and *C. nigrifrons* and *C. caerulus* those of *Lipoptena hopkinsi.* That keds have not been reported thus far from other duikers is presumably due to insufficient collecting.

c. The Hippotraginae are large to very large, mainly African antelopes, with a few representatives in southwestern Asia. Of the 13 Recent genera recognized by Simpson (1945), 7 have no known hippoboscids: *Onotragus* (2) or lechwe, *Pelea* (1) or Vaal rhebok, *Hippotragus* (3) or roan and sable antelopes and blaauwbok, *Oryx* (3) or gemsbok and white oryx, *Addax* (1) or addax, *Connochaetes* (1) or gnu, and *Beatragus* (1) or Hunter's antelope. Of the remaining 6, 4 harbor *Hippobosca* and 3 *Echestypus* (Melophaginae). *Kobus* (2), the waterbucks, are regularly infested with *Hippobosca hirsuta,* on both *K. ellipsiprymnus* and *K. defassa;*

while *Echestypus paradoxus* has been taken accidentally on *K. ellipsiprymnus.* Of the 2 species of *Adenota,* the kobs and pukus, one, *A. vardoni,* is a regular host of *Hippobosca hirsuta.* For *Redunca* (3), the reedbucks, there is only one record of *Echestypus paradoxus* from *R. arundinum,* possibly based on a stray. Previously no flies had been reported from *Damaliscus* (4); but I have recently seen specimens of *Echestypus sepiaceus* labelled as taken from *D. korrigum,* the topi, in Kenya, by Mr. W. Phillips. In *Alcelaphus* (3), the hartebeests, *A. lichtensteini* is the type host of *Hippobosca fulva.* The single species of *Gorgon, G. taurinus,* the blue wildebeest, was reported as a wild host of *Hippobosca rufipes* in the Transvaal by Bedford (1927, p. 782).

d. The Antilopinae comprise both large and small antelopes and range over most of Africa, as well as over a wide territory in Asia. No flies have been reported from 7 of the 15 Recent genera listed by Simpson (1945): *Oreotragus* (1) or klipspringer, *Neotragus* (2; including *Hylarnus*) or royal antelopes, the smallest of the living Artiodactyla, *Madoqua* (5) or dikdiks, *Dorcatragus* (1) or beira, *Antilope* (1) or blackbuck, *Ammodorcas* (1) or dibatag, and *Litocranius* (1) or gerenuk. Except for *Antilope,* of Central Asia, these genera are African. Of the remaining 8 genera, 5 are reported as hosts of *Hippobosca,* 5 as hosts of *Echestypus* and 2 as hosts of *Lipoptena;* but some of the cases may be accidental or even open to question. Only one is strictly Asiatic, *Procapra* (2), of which one species, *P. gutturosa,* the zeren, is the type host of Pallas' (1777) *Lipoptena antilopes,* a ked not seen again for the past 150 years. *Gazella* (16) occurs both in Africa and Asia, but flies are known only from a few of the African species, possibly due to lack of interest. *Echestypus sepiaceus* was definitely taken on *G. rufifrons, G. tilonura,* and *G. thomsonii;* possibly also on *G. granti* (E. A. Lewis' supposed *Lipoptena cervi* in Kenya; see J. Bequaert, 1942*a*, p. 149). The following genera are strictly African. *Aepyceros,* with one species, *A. melampus,* the impala, a true host of *Hippobosca fulva* (= *H. martinaglia*), but probably a stray host only of *Echestypus paradoxus.* In *Ourebia* (3), *O. ourebi,* the oribi, is one of the regular hosts of *Echestypus sepiaceus. Antidorcas* (1) *marsupialis,* the springbok, and *Raphicerus* (3) *campestris,* the steinbok, are both known as hosts of *Hippobosca rufipes* and *Echestypus binoculus.* In *Nesotragus* (2), *N. moschatus,* the suni or dwarf antelope, is possibly a true breeding host of *Lipoptena hopkinsi,* though there is only one record thus far. *Rhynchotragus* (3), the long-snouted dikdiks, have no known specific fly. The reported occurrences of *Hippobosca longipennis* on *Rhynchotragus* and on some of the gazelles will be discussed later.

e. The Caprinae, or sheep, goats, chamois and their relatives, are mainly European and Asiatic, with a few species in North Africa and western North America. They are mostly medium-sized, often covered with a long and dense fur, sometimes in addition with a thick under coat of wool. In nature most of them select a mountainous habitat. Simpson (1945) recognizes 13 Recent genera, of which the following 9 have no known flies: *Pantholops* (1) or chiru, *Saiga* (1) or saiga, *Naemorhedus* (1) or goral, *Oreamnos* (1) or Rocky Mountain goat, *Budorcas* (1) or takin, *Ovibos* (1) or musk ox, *Hemitragus* (3) or tahr, *Pseudois* (1) or bharal, and *Ammotragus* (1) or audad. The five Hippoboscidae found on the remaining 4 genera are all Melophaginae. *Rupicapra,* with the single species *R. rupicapra,* the chamois or gemse of Europe and Asia Minor, has two of them, *Melophagus rupicaprinus* and *Lipoptena couturieri.* The reported occurrence of *Melophagus ovinus* on chamois, by Massonat (1909, p. 263) and others, was clearly based on specimens of *M. rupicaprinus,* as Falcoz (1926, p. 40) pointed out. Fiebiger (1923, *Tierischen Parasiten Haus- u. Nutztiere,* 2nd Edition, p. 400; copied by Hase, 1940, p. 644) includes the chamois among the hosts of *Lipoptena cervi;* but this was evidently based on hunters' reports and due to a confusion with either *Melophagus rupicaprinus* or *Lipoptena couturieri.* In *Capricornis* (2), the dwarf serow of Japan, *C. crispus,* has the specific *Lipoptena japonica.* The Old World genus *Capra* (6) includes the goats, ibexes, markhor, and tur. I expect that several of these animals will eventually be found to harbor hippoboscids. Thus far, however, flies are known in nature only from three races of *Capra ibex,* the ibex. *Lipoptena chalcomelaena* is definitely recorded from *Capra ibex nubiana,* the Nubian ibex, and *C. i. sinaitica,* the Sinai ibex. Speiser (1905*a,* p. 354) reported it also from *Capra hircus aegagrus,* presumably the wild ancestor in Asia Minor of the domestic goat; but he may have confused it with *L. capreoli,* which he seems not to have recognized. Goidanich (1951) recently reported the interesting discovery in Italy on *Capra ibex ibex,* the European ibex, of *Melophagus rupicaprinus,* a ked known previously only from chamois. *Lipoptena capreoli* is a common parasite of domestic goats in the Near East (Dalmatia, Greece, Cyprus, Asia Minor, Palestine) and northwestern India; but it is not known at present from a wild host (see below). Although it strays sometimes to camels, cattle or dogs, it seems to avoid sheep, according to

Aschner (1931). On the other hand, the sheep-ked, *Melophagus ovinus,* occurs sometimes on goats, where they mingle with sheep. Just how to interpret Speiser's record (1908*c,* p. 444) of his *M. ovinus* var. *fera* from a "Steinbock," in the Caucasus, must be left undecided. *Ovis* (6) contains, in addition to the domestic sheep, wild species in southern Europe, Asia and western North America. The occurrence of *Melophagus ovinus* on various breeds of sheep in domestication will be discussed later. It should be pointed out here that evidence of its living at present on wild sheep is as yet very meagre. It is based on one record of 2 keds taken from a museum skin of *Ovis ammon polii,* the Marco Polo sheep, and needs confirmation from a more reliable source (J. Bequaert, 1942*a*, p. 186). I reached the conclusion previously (1942*a,* pp. 187 and 203) that *M. ovinus montanus,* described by Ferris and Cole (1922, p. 192) from North American "mountain sheep" (presumably *Ovis canadensis* or *O. dalli*), was based on ordinary sheep-keds that had strayed from feral domestic sheep. There is actually no fully reliable evidence that the native American sheep are normally infested with keds.

I have discussed the Artiodactyla at some length, even listing all known Recent genera, because of the interesting aspects of the host relations of their flies. I pointed out before the decided preference shown by the Hippoboscidae for this order. Of the 8 genera and 34 species of mammal-infesting flies, no less than 5 genera and 28 species use Artiodactyla as regular breeding hosts, and of these only 3 species of *Hippobosca* breed also on Perissodactyla in domestication. Within the order, the known hosts belong to a variety of types, since they represent 4 of the 8 families and 34 of the 76 genera. The diversity of types known to carry flies strongly suggests that several additional breeding hosts will be discovered among the genera from which such parasites have not yet been reported.

It appears from the foregoing review that, disregarding possible accidental records, the Hippoboscinae (*Hippobosca*) select as breeding hosts within the order only a few of the Camelidae and of three subfamilies of Bovidae, the Bovinae, Hippotraginae and Antilopinae. These flies furthermore, seem to prefer animals of large size (*Camelus;* domestic cattle, probably an acquired host; *Taurotragus; Kobus; Adenota; Alcelaphus; Gorgon;* and *Aepyceros*). On the other hand, the Melophaginae (*Melophagus, Lipoptena, Neolipoptena,* and *Echestypus*) have a much wider host range, possibly due to their greater specific variety, since they are known to breed on Tragulidae, Cervidae and all five subfamilies of Bovidae. As I mentioned before (1942*a*, p. 33), the ked-flies seem to favor small or medium-sized hosts among the available Artiodactyla: *Capreolus, Cervus, Mazama, Muntiacus, Axis, Moschus, Odocoileus,* the smaller species of *Strepsiceros, Cephalophus, Sylvicapra, Antidorcas, Gazella, Nesotragus, Ourebia, Raphicerus, Capra, Ovis, Capricornis,* and *Rupicapra.* Apart from strays or doubtful records, the only notable exceptions to this rule are the occurrences of *Lipoptena cervi* on *Alces,* of *Echestypus paradoxus* on the larger *Strepsiceros,* and of *Lipoptena antilopes* on *Procapra.* It may be noted in this connection that the larger Artiodactyla tend to congregate in herds, while the smaller types live more often singly or in pairs; although it is difficult to see how this ecological peculiarity might have influenced a preferential host choice extending to most of the species of one subfamily.

Hippoboscidae of Domesticated Hosts and Their Origin. For the purpose of the present discussion, the term ''domestication'' will be given a definite, restricted meaning. It involves more than merely converting a wild animal to domestic uses, a definition which covers also most birds and mammals kept in captivity, either more or less tamed or as pets. There is, of course, every gradation between ''taming'' and complete ''domestication''; while even the most thoroughly domesticated animal may revert to a wild or so-called feral state under suitable circumstances. The two fundamental features of true domestication are that the animals depend for their welfare upon association with Man and breed continuously in confinement. Man now directs their feeding, shelter, and reproduction, and influences their structure, physiology and even behavior, mainly by controlled breeding. Taking advantage of the ever-present intra-specific variation, he has produced or maintained, by deliberate selection and crossing, the numerous races or breeds so characteristic of all truly domesticated animals. The human impact has caused profound departures from the original features of the wild ancestral stock. The most interesting change from our point of view is a lowered resistance against adverse factors in the environment, particularly against diseases and parasites. When domestic animals carry Hippoboscidae, the fly populations tend to be larger than those of the same or closely related species on wild hosts. This may be due in part to indolence acquired by the sheltered life, the animal no longer attempting to rid itself of the flies, and to some extent also to changes in the physical characteristics of the plumage or fur, deliberately produced by Man for economic or esthetic reasons. Furthermore, the close association of the hosts in flocks or herds, particularly when kept in well-sheltered quarters, seems to increase the reproductive potential of the flies, were it only by securing a host for nearly every emerging adult.

Few Hippoboscidae use domesticated animals as regular breeding hosts. The problem of where these flies came from and at what time and in what part of the world they became established on domestic hosts is difficult to approach. Obviously they were either retained from an original wild ancestral host or acquired after domestication from some other wild or domestic animal. Moreover, it is not impossible, though difficult to prove, that the domestication of the host may have induced in some cases, by indirect selection, changes in the structure and behavior of the parasite, which now mask its true affinities. The chief difficulty of the subject, however, is the present unsatisfactory knowledge of the ancestry of nearly all domestic animals. To add to the uncertainty, most flies of domestic mammals are not known at present to breed regularly on any Recent wild host, presumably because the original host became extinct since domestication started.

Of the several birds now kept in domestication, only the pigeon is regularly infested with a specific hippoboscid. *Pseudolynchia canariensis* has become a nearly cosmopolitan pest of domestic pigeons in the tropical and subtropical parts of the World, being transported by Man with the host. The numerous domestic races of pigeons are all derived from the wild rock dove, *Columba livia,* several subspecies of which inhabit the British Isles, the southern Palearctic Region, the Sahara, the Sudan and southern Asia. The behavior of this bird in the wild state has certain features which made it suitable for domestication, such as gregariousness, a strongly developed homing instinct, and the habit of nesting in sheltered places and not in trees. Nowadays the wild *Columba livia intermedia* commonly enters human dwellings to nest in India, where quite possibly domestication may have originated. There is, however, little precise information on when and where pigeons were first consistently kept and bred by humans. Dr. Robert J. Braidwood, of the Oriental Institute, the University of Chicago, has kindly called my attention to information possibly bearing on this subject, in so far as it concerns ancient Egypt and Mesopotamia. R. Lepsius (1849–1856, *Denkmäler aus Aegypten*) published a relief on the pyramids of Saqura, dating from the Fifth Dynasty of the Old Egyptian Empire (*circa* 2500 B. C.), showing several pigeons together with other domestic birds (Abt. II, vol. **3**, pl. 70);

and another of a later date, in the Twentieth Dynasty of the New Empire (*circa* 1200 B. C.), depicting an attendant at a religious ceremony releasing 4 pigeons (Abt. III, vol. 7, pl. 213; reproduced by Boussac, 1911, *Rec. Trav. Relat. Phil. Arch. Egypt. Assyr.*, **33**, p. 63, fig. 9). With regard to Mesopotamia, it seems fairly certain, according to Dr. Braidwood, that by *circa* 2500 B. C. when Sumerian texts are available in some quantity, a differentiation was made in the current language between ''wild'' and ''tame'' pigeons and dovecotes were mentioned in connection with the Sumerian temples.

That the *Pseudolynchia* was retained from the wild rock pigeon can scarcely be doubted, since it has actually been taken in nature on the Indian *C. livia intermedia* (Ansari, 1947, p. 511; 1949, p. 216) and is by no means rare on several related wild Columbidae in Africa. The parasite remains with the feral pigeons that thrive in some of our larger cities. An interesting feature of *P. canariensis* is a tendency of the fly to grow somewhat larger on domesticated birds than on wild pigeons and doves or on other natural hosts. The length of the wing averages about 5 mm. on wild hosts and about 6 mm. in domestication. The fly evidently finds more favorable conditions in the domesticated state, which is further shown by the large numbers present on the squabs in the dovecotes and pigeon lofts, contrasting with its scarcity on wild birds.

The ostrich, occasionally kept semi-domesticated in South Africa, harbors a specific fly, *Hippobosca struthionis,* which apparently occurs as often on controlled as on fully wild birds. Information on the ecology of this parasite is practically lacking, so that it cannot be ascertained to what extent it has been affected by human interference.

In view of the far-flung wanderings in Man's company of the domestic fowl, it is remarkable that these birds are very exceptionally infested with hippoboscids, although they have many other ectoparasites. All the numerous breeds of fowl are, it is agreed, descended from a single ancestral wild species, *Gallus gallus,* indigenous to southern Asia, Sumatra and Java. In the section dealing with the bird-flies of the Galliformes, I have mentioned *Lynchia* (*Ornithophila*) *maquilingensis* as occurring on wild fowl in Burma and Java, as well as the accidental captures of various other flies either on fowl gone feral or in domestication. So far as known, however, fowl kept in domestication are never regular breeding hosts of any fly.

I have mentioned before the one known record of *Ornithomyia* *avicularia* from a domesticated peacock, the ancestral stock of which, *Pavo cristatus,* occurs in India and Ceylon, where no bird-fly has been found on it thus far.

The domestic turkey deserves to be considered at greater length. It seems to be generally agreed that it was derived from the wild *Meleagris gallopavo,* which originally inhabited much of the United States and Mexico. It was found domesticated among the Mexican Indians by the Spanish, who carried it to the Old World. Thus far no hippoboscid has been reported from wild turkeys in Mexico; but in the southeastern United States *Lynchia americana,* a common fly with little host preference, has been taken on a few occasions from the local wild subspecies, *Meleagris gallopavo silvestris,* which may well be one of its several true breeding hosts. No louse-fly has been reported thus far from domestic turkeys either in North America or in the Old World. In South America, however, Lutz, Neiva and da Costa Lima (1915, p. 179), as well as Lutz and Penna (1918, *Mem. Inst. Osw. Cruz,* **10**, p. 85), reported *Olfersia coriacea* (= *Pseudolfersia meleagridis*) from domestic turkeys ("perú domestico") in northeastern Brazil (Pernambuco and Maranhão), a part of the New World outside the original range of the wild turkey. I have seen some of these flies, as well as others taken on domestic turkeys in Rio Grande do Norte, Brazil, and they are unquestionably *O. coriacea.* Further investigation must be awaited to decide whether or not *O. coriacea* has adopted the domestic turkey as a new breeding host; otherwise it is a specific parasite of native American game birds of the family Cracidae (guans, curassows, and chachalacas), as well as of the wild ocellated turkey (*Agriocharis*). I have seen one *Stilbometopa podopostyla* labelled as taken on a domestic turkey in Goyaz, Brazil.

I find no records of hippoboscids from other domesticated birds, such as ducks, geese, guinea-fowl, and canary-birds (Fringillidae). In the case of ducks and geese, this is not too surprising, since, as noted before, the order Anseriformes, to which these birds belong, is almost completely shunned by louse-flies in nature. The native African *Numida meleagris,* the ancestor of the domestic guinea-fowl, is generally free of flies. Thus far I have seen only two pigeon-flies, *Pseudolynchia canariensis,* from wild guinea-fowl in Uganda and Somaliland, presumably accidental strays. It might be interesting to inquire whether in the Greater Antilles, where the West African race, *Numida meleagris galeata,* was introduced, some of the common local hippoboscids did not become established on the feral birds.

The following hippoboscids use domestic mammals as regular breeding hosts: *Hippobosca longipennis* (= *H. capensis; H. canina*) on dogs; *H. equina, H. variegata* (= *H. maculata*) and *H. rufipes* (= *H. camelopardalis*) on equines and bovines; *H. camelina* (= *H. bactriana; H. dromedarina*) on camels and dromedaries; (For a full synonymy of *Hippobosca,* see J. Bequaert, 1931, 1939*b*, and 1941*a*); *Melophagus ovinus* on sheep; *Lipoptena capreoli* (= *L. caprina*) on goats. This list does not include of mammals now kept in domestication the cat, pig, rabbit, llama, alpaca, guinea-pig, and elephant, which are not known to harbor louse-flies, except perhaps as temporary strays. The flies of domestic animals belong to 2 subfamilies and 3 genera (Hippoboscinae: *Hippobosca;* Melophaginae: *Melophagus* and *Lipoptena*), which (except for *Hippobosca struthionis*) comprise only strictly specific parasites of mammals. Bird-flies stray very rarely to such hosts, probably not more often than to Man.

In discussing the origin of the flies of domestic animals, I have generally followed thus far C. Keller's (1902) work on the ancestry of these hosts. However, this being now superseded by more recent investigations, I accept at present most of the conclusions reached by O. Antonius (1922), unless the results of more recent researches seem more reliable.

Hippobosca longipennis Fabricius, the dog-fly, presents some interesting problems. Its origin is fairly clear, since, as shown before, it has even nowadays several wild breeding hosts among the African Carnivora. It must be stressed that *H. longipennis* is a valid species, neither cospecific with *H. equina,* as Ferris (1930*b*, p. 541) claimed, nor merely subspecifically distinct. *H. equina canina* Drensky (1926, p. 98), proposed as a new subspecies from dogs in Bulgaria, is a synonym of *H. longipennis,* which was previously described as *H. canina* by Rondani (1878). I pointed out (1939*b*, pp. 77 and 79) that, in addition to the better known differences in size and color, there are others in the chetotaxy of the scutellum, the shape of the abdominal tergal plates and the apical lobes of the frons. The two species differ in characters of the same value as those used to differentiate other closely allied hippoboscids. *H. equina* and *H. longipennis* appear to be not more nearly related to each other than to *H. fulva,* these three species forming a compact group within the genus *Hippobosca.* This conclusion is supported by the different host specificity and peculiar distribution of each species. Under domestication, *H. longipennis* is highly specific to the dog as a breeding host. The few records of temporary straying to other domestic and wild hosts are reviewed below. On the whole, this species does not seem to attack other animals more readily than it does Man. It is particularly interesting that it was never found on the domestic cat, although it is a regular parasite of several East African wild felines.

The wild breeding hosts of *H. longipennis,* discussed in the section on Carnivora, include jackals, foxes, civets, hyenas, cheetahs, servals, leopards and lions. They are known thus far mainly from Upper Egypt (Luxor) and East Africa (Somaliland, Kenya, Uganda, and Tanganyika), where the fly is abundant at all seasons and where it seems to be rarer on domestic dogs than on the wild hosts. According to Falcoz (1926, p. 29), Surcouf took it also on a jackal in Algeria. On domestic dogs the fly extends over a much wider area than in nature, there being reliable records for most of the Mediterranean Subregion (Spain, Italy, Bulgaria, Greece, Crimea, Asia Minor, Transcaucasia, Transcaspia, Turkestan, Iran, Iraq, Syria, Palestine, Cyprus, Egypt, Cyrenaica, Libya, Sicily, Sardinia, Tunis, Algeria, and Morocco), the Cape Verde Islands, Senegal, French Guinea, Northern Nigeria, eastern Sudan, Eritrea, Somaliland, Kenya, Zanzibar, Uganda, Tanganyika, Portuguese East Africa (as far south as Lourenzo Marques), Transvaal, Southwest Africa, Arabia, India, Ceylon, Assam, Burma, Afghanistan, Indo-China, south and central China, Hainan, Formosa and southern Korea. There are a few Old World records outside this range, in Central Europe (Hungary, Poland, Tirol, Germany), northern China (Harbin; Tarhanwangfuo), Japan (Kanagawa), Java (one specimen seen), and the Cape Province of South Africa (Grahamstown); but they are most probably due to temporary imports on infested dogs, there being no evidence that the parasite is definitely established in any of these places. I have given the distribution in detail to show how restricted it is as compared with that of the host, which is now as nearly cosmopolitan as any mammal could be. Most probably the present extension of the fly's range was reached early in the history of the domestic dog. Elsewhere (1939*b*, pp. 80–81) I have cited some references to dog-flies in the ancient Greek literature (before 800 B. C.) and Chinese writings (1200 to 1600 A. D.). Why the parasite did not spread farther, following the extensive wanderings of the host, is difficult to understand, particularly in view of the fact that some other ectoparasites of dogs are now almost universal. The present-day restricted distribution can hardly be accounted for by climatic factors, since the fly must have been carried occasionally with dogs to New World areas with a suitable climate where it failed to become established. Nevertheless, it is worthy of note that it avoids the cold temperate and arctic regions, as well as the parts of the Old World with a hot and humid tropical climate. There is a possibility that the presence of flies may be correlated with some peculiar local habits of the host. In the Near East, India and parts of China, the flies often swarm on the street and pariah dogs, which live freely and in packs, more under conditions approaching presumably those of the wild ancestors. The flies perhaps avoid certain races of dogs; or possibly very close association with Man and the permanent sheltering of the host in human dwellings or in kennels may interfere with the fly's normal life history.

Only the domestic dog and certain wild African Carnivora should be regarded as effective breeding hosts of *H. longipennis;* but there are many accidental records from other types of hosts, as the following critical review will show. Waterston (1918, *Bull. Ent. Res.,* **9**, p. 155) took one fly on a mule in Macedonia. Two females were taken on cattle in Portugal by Braga (1942, p. 379); although it is strange that the fly was not mentioned by him from dogs in the same area. I received a specimen taken on a cow in Cyprus by G. Mavromoustakis. Glasgow (1946, pp. 93–103) reports that it came regularly to a bait ox led over the bush trails near Mpwapwa, Tanganyika, up to 26 flies being caught in one day; I find no other notice of its living on cattle in East Africa. Speiser's (1915, p. 3) record from a dikdik, *Rhynchotragus kirkii minor*, in Kenya, and Lewis' (1931, *Ann. Rept. Dept. Agric. Kenya* for 1930, p. 162) from a Grant's gazelle, *Gazella granti,* also in Kenya, might well have been due to a confusion with *H. fulva.* However, I have seen a male of *H. longipennis* taken on a Thomson's gazelle, *Gazella thomsoni,* 75 miles west of Narok, Kenya, by Dr. N. A. Weber, in January, 1948; and another fly found on an unidentified gazelle at Sana, Yemen, 7000 ft., by H. Scott and E. B. Britton. Loveridge's record from a duiker, *Sylvicapra grimmia,* which I quoted in 1931 (p. 316), was erroneous, being based on *Echestypus paradoxus.* I was unable to find real evidence for the supposed occurrence on the dromedary (Falcoz, 1926, p. 29). Giglioli (1864) described his *Ornithomyia chinensis* (a synonym of *H. longipennis*) from a thrush, *Turdus obscurus,* in China, possibly through some error or contamination. A more reliable record from a bird is an unfed female taken by R. Meinertzhagen on *Passer h. hispaniolensis,* at Sous, Morocco, in November, 1939. The reported attacks on Man will be discussed later.

The domestic dog, *Canis familiaris,* appears to have been the first animal domesticated by primitive Man, presumably during the long period when hunting was the chief source of human food. The earliest positively recognizable remains of a dog, *Canis putianini,* found in Central Russia in association with human implements, date from the very early Neolithic (probably Campignian, 6000 to 10,000 B. C.). According to Antonius (1922, pp. 132–138), this animal had all the characteristics of the genus *Canis,* proper, which includes the jackals, wolves and coyotes. He also claims a monophyletic origin for all the many breeds of dogs now kept by the different races of mankind, although he admits that occasional crossing with other species of *Canis* may have added some peculiarities. He regards as the most probable ancestor one of the small wild Mediterranean races, possibly now extinct, of the common wolf, *Canis lupus.* Such wild races have survived in various parts of southern Europe, North Africa and Asia Minor. Whether *Hippobosca longipennis* lived on this ancestral wolf is pure conjecture, since the fly has never been taken on any of the surviving races of *C. lupus.* It could equally well have been acquired after domestication, but in the original area, from some jackal-like species of *Canis,* with which the dogs may have associated from time to time, and some of which are known at present as wild hosts of the fly.

Other hippoboscids, particularly *Melophagus ovinus,* are occasionally found on domestic dogs as accidental and temporary strays. The few published records of *Hippobosca equina* or *H. variegata* straying to dogs are discussed below.

Hippobosca equina Linnaeus and *H. variegata* Megerle v. Mühlfeld have certain ecological features in common which make it advisable to discuss them jointly. Neither of them has at present a known effective wild breeding host. Both are frequent parasites in certain parts of the Globe of domestic equines and cattle (possibly including the water buffalo), without showing a decided preference. They are sometimes common on such hosts that return to the feral state. As they are usually abundant and as they emerge away from the hosts, they are apt to stray to other mammals or even to birds. The records of abnormal hosts should be considered critically, lest they lead to erroneous conclusions.

In a valuable paper, which I have frequently quoted, Hase (1927*b,* p. 212) lists as casual hosts of *H. equina* the dog, pig, domestic rabbit, hare, dromedary, wisent, red kite and little owl. The earliest mentions of this fly on dog by Scopoli (1763, *Entomologia Carniolica,* p. 376), Fourcroy (1785, *Entomologia Parisiensis,*

2, p. 504), P. Rossi (1790, *Fauna Etrusca,* **2**, p. 337), and others should perhaps be ignored, since the true dog-fly, *H. longipennis,* was not at that time usually recognized as distinct from *H. equina.* There is doubt also about some later references by F. Rossi (1848, *Syst. Verzeichn. Zweifl. Ins. Oesterreich,* p. 85), R. Blanchard (1890, p. 494), Kishida (in Esaki, 1932, p. 243), Bezzi (1905, p. 274), and Falcoz (1926, p. 28), most of which are clearly not based on original observations. Actually I can find only four precise and seemingly reliable records: (1) Réaumur (1742) stated that in central France, where *H. longipennis* is not known to occur, *H. equina* was sometimes found on dogs; (2) Massonat (1909, p. 242) reports 10 specimens from dogs in the Algerian Sahara; (3) Sergent and Foley (1910, *Bull. Soc. Path. Exot., Paris,* **3**, p. 482; as *H. equi*) took some on dogs in the western Algerian Sahara (south of Oran); (4) I reported (1931, p. 310) from Banyuls-sur-Mer, southern France, a specimen at the Museum of Comparative Zoology, labelled as taken on a dog, May 20, 1882, by G. Dimmock. The notice of the domestic pig as a host was traced to R. Blanchard (1890, p. 494), but the record is very vague and possibly fictitious. The claims for *H. equina* occurring on the domestic rabbit and the hare are also unsatisfactory; they seem to have originated from a general listing of hosts by Bezzi (1905, p. 274). At any rate, I was unable to find earlier or more precise information, and the later references by Grünberg (1907, *Die Blutsaugenden Dipteren,* p. 180), Klugkist (1909, p. 542), Falcoz (1926, p. 28), Reichert (1939, p. 83), and Ullrich (1939, p. 2169) seem to be repetitions of Bezzi's statement. Massonat (1909, p. 242) mentions that many *H. equina* were taken from a dromedary in the Algerian Sahara (Beni-Ounif). I have seen several specimens collected on a camel at Reshadie near Smyrna, Asia Minor, in August, 1928, by H. R. Hagan, and one fly from the same host taken in July, 1948, at Pangao, Afghanistan, by N. Haarlöv. Hase credits the occurrence of *H. equina* on the wisent, *Bison bonasus,* to Nöller; but actually Wrublewski (1912, p. 384) found it on one of the few remaining wisents in the forest of Bielowieza, Poland. This find is most interesting in view of the possibility that the wisent may have been one of the original wild hosts; but, as this animal is now near extinction, it is certainly no longer an effective host. I have seen one *H. equina* labelled as taken by P. Franck at Tjikepoe, Venatoria Estate, S. W. Java, from a banteng, *Bibos banteng,* presumably in domestication. An additional interesting host is the domesticated water buffalo, *Bubalus bubalis,* included by Babić and Baranov (1935, pp. 158–159) among the hosts of *H. equina* in Jugoslavia. Mégnin (1899) stated that

H. equina occurs sometimes in France on domestic sheep; several specimens were received from Dr. Bilal Golem from two localities in Asiatic Turkey (D. Bakir and Bitlis), with a notice that they came from domestic sheep. Johnsen (1948, p. 280) records one *H. equina* taken on the roebuck, *Capreolus capreolus,* in Jutland, Denmark. This fly strays occasionally to birds also. F. Rossi (1848, *Syst. Verzeichn. Zweifl. Ins. Oesterreich,* p. 85) states that Natterer found it on the European pigmy owl, *Glaucidium passerinum,* near Vienna, Austria. Massonat (1909, p. 242) reports one female from a European red kite, *Milvus milvus,* near Villars, Department of Ain, France; and 8 specimens (4 ♀ and 4 ♂) from the European little owl, *Athene noctua,* in the same locality, possibly from different individuals. Schuurmans Stekhoven (1923, table III) mentions a specimen found on domestic pigeon at Djetis, Java. Bau (1929*b*, p. 9) lists one from "*Corvus graculus* L.," in Europe, without more precise locality; he believes that this bird was *Phalacrocorax graculus,* the cormorant or "Krähenscharbe"; more probably the name was intended for the mountain chough or "Alpendohle," *Pyrrhocorax graculus* (Linnaeus), which was originally described as *Corvus graculus.* Falcoz (1931, p. 42) reports *H. equina* from a "heron" in the Senegal. I have seen an unfed, teneral male taken on a dunlin, *Erolia a. alpina,* in November, 1939, at Sous, Morocco, by R. Meinertzhagen. Occurrences on Man are analyzed in the sequel.

No doubt owing to its restricted distribution in the tropics of the Old World, *H. variegata* has been seldom taken on abnormal hosts. The supposed occurrence on an African antelope (Neave, 1911, *Bull. Ent. Res.,* **1**, pt. 4, p. 313) was due to failure to recognize *H. hirsuta.* Bezzi (1914, *Redia,* **10**, pt. 2, p. 230) mentions specimens taken on camels in southern Somaliland; Edwards (1932, *in B. Thomas, Arabia Felix,* p. 363) reports it from the same host in southeastern Arabia; and Lewis (1931, *Ann. Rept. Dept. Agric. Kenya* for 1930, p. 162) also on camels from the Northern Frontier District of Kenya. Schuurmans Stekhoven (1923, p. 73) found *H. variegata* on domesticated water buffalo, *Bubalus bubalis,* in Sumba, Indonesia; and I have seen a specimen taken from the same host at Kurumbaragam, southern India, by P. S. Nathan. The possibility that the water buffalo or carabao may be an effective breeding host should be investigated. Even more surprising is Schuurmans Stekhoven's statement that this fly was common on sheep and goats in the islands of Rotti and Savu, Indonesia; he counted some 60 flies per head in a herd of these animals at Termanoe on Rotti.

He also remarks that a fly occasionally settled on a dog in Sumba. I have a specimen labelled as taken from a dog at Taveta, Kenya. It is not certain, however, that in both these cases *H. variegata* actually did bite the dogs. Occurrences on Man will be reviewed later.

The present-day distribution of the two flies shows some striking differences. *H. equina* is well established, either in domestication or on domestic hosts gone feral, throughout nearly the whole of the Palearctic Region and in certain other limited areas of the Old World. There are reliable records from England (a few localities in Hampshire, Dorset, Devon and Carnarvonshire, often on feral hosts; probably only through accidental importation elsewhere), Sweden, Norway, Denmark, most of Russia, Finland, Siberia, Germany (a few localities, particularly on moors), Switzerland (very few localities), Austria, southern and central France, Portugal, Spain, the Baleares, Italy, Corsica, Sardinia, Sicily, Jugoslavia, Albania, Hungary, Roumania, Bulgaria, Greece, Turkey-in-Europe, Asia Minor, the Caucasus, Transcaspia, Iran, Turkestan, Syria, Palestine, Cyprus, Creta, Rhodes and other islands of the Archipelago, Egypt, Cyrenaica, Libya, Tunis, Algeria, Morocco, Canary Islands, Madeira, Azores, Cape Verde Islands (rather doubtful), the eastern Sudan, Arabia, India (a few localities), Afghanistan, Singapore, Indo-China (Annam), Siam, the Philippines, some of the Sunda Islands (Flores, Sumbawa, Lombok, Saleyer, Bali, Java, Madura, Sumatra), Celebes, Amboina, Fiji, the New Hebrides, Loyalty Islands, and New Caledonia (introduced about 1890, now abundant; also in the Isle of Pines). It is very sporadic in western Europe. In the Netherlands, Belgium, northern France and most of Germany it now occurs only on horses recently imported from infested areas farther south. It is not now established in Africa south of the Sahara and in the New World, in spite of occasional introductions on infested horses or cattle from elsewhere. I am also unable to find reliable records from China, Mongolia, Japan, and Formosa. Although imported accidentally from time to time in Australia, it has only become established in a few localities there (Seddon, 1951, p. 111). This distribution has two striking peculiarities. First, *H. equina* is decidedly northern or boreal, apparently able to survive in the open throughout the winter very far north, perhaps close to the Arctic Circle in Lapland. Contrasted with this is its absence from much of the African Continent and its failure to invade Australia and America. It is difficult to account for these vagaries by climatic factors alone; although the fly is probably averse to truly tropical conditions, with extremes of high temperatures and high humidity. That it thrives in some of the Malaysian and Pacific Islands may be due to their insular climate. Moreover, *H. equina* is rather scarce in the Sunda Islands and Schuurmans Stekhoven (1923) failed to find it in some of them (Sumba, Rotti, Timor), where *H. variegata* is common.

Hippobosca variegata (= *H. maculata*) occupies a much smaller territory. It is reported as well established on equines or cattle in Egypt, Mauritania, the Sudan from the Senegal to the Red Sea, Sierra Leone, French Guinea, Gold Coast, Dahomey, Northern and Southern Nigeria, northern Cameroon, French Equatorial Africa (Chad, Ubangi), Eritrea, Abyssinia, Somaliland, Uganda, Kenya, Tanganyika, Zanzibar, Portuguese East Africa, Transvaal, Mauritius, Reunion, Madagascar, Comoros, Seychelles, Andaman Islands, southern Arabia, Iraq, Iran, India, Ceylon, most of the Sunda Islands (Timor, Sumba, Rotti, Flores, Java, Savu), Celebes and the Philippines. I can find no definite record from China or Japan, although it has been included in some general accounts of Chinese and Japanese biting insects. There are a very few records from the French Congo (Brazzaville) and Belgian Congo (Loka; Sankuru District), probably of flies from horses or cattle freshly imported from normally infested areas. In contrast with *H. equina*, *H. variegata* is a tropical insect, but with a preference for relatively dry areas or possibly for more open grassland or wooded savanna. It is also partial to insular conditions, so that its area overlaps that of *H. equina* in the Indonesian Islands. According to Schuurmans Stekhoven (1923), in the Sunda Islands *H. variegata* has a wider distribution and is more abundant on the hosts than *H. equina*. I cannot find definitely stated that both species were ever found on the same individual equine or bovine.

Wherever they occur, both *H. equina* and *H. variegata* infest nowadays all domestic equines, horses, donkeys, mules and hinnies, without particular preference. They have, however, not been found, even as strays, on any of the living wild Equidae, such as the wild horses and onagers of Asia and the zebras of Africa, which have no known hippoboscid parasites. The ancestry of the domestic horse, *Equus caballus*, has led to much controversy and full agreement has not been reached in the matter. In his recent comprehensive work, B. Lundholm (1949) regards the earliest European domestic horses as monophyletic, in the sense that all were derived from a single wild species, which persisted sporadically in Europe far into historic times, but is now extinct. As these early domestic horses are not an homogeneous group, taming and later true domestication must have started independently in several areas, in each of them from a different race of the wild *Equus caballus*. These conclusions are based on a comparative study of fossil late Pleistocene remains and of skeletons of the earliest true domestic horses of the Bronze Age in Europe. Taming, followed later by true domestication, most probably occurred in the very late Stone Age (late Neolithic, *circa* 5000–3500 B. C.). From eastern Europe domestic horses were introduced to western Asia and Egypt at a later date (*circa* 2000 B. C.).

It is generally agreed that the domestic ass or donkey was derived from a wild ancestor, *Equus* (*Asinus*) *asinus*, which formerly inhabited Northwest Africa, the eastern Sudan and Northeast Africa. It occurred throughout most of this area in several races within historic times, but survives now only in Somaliland. Domestication occurred in late Neolithic times at the earliest (*circa* 3500 B. C.), presumably in Egypt. It spread soon afterward to Asia Minor and Mesopotamia, where the breeding of mules and hinnies was started at a much later period after domestic horses were introduced from Europe.

Five distinct main types of bovines are now kept in domestication in different parts of the World, but one of them far outweighs the others in economic importance and is, moreover, the most important from our present viewpoint. In the highlands of Central Asia, the yak, *Bos* (*Poephagus*) *grunniens*, is an important domestic animal, derived from a local wild ancestor, but has never spread beyond the original home; no hippoboscid is known from it. The water buffalo, *Bubalus bubalis*, whose wild ancestor was a native of India, Indo-China and Borneo, has spread in domestication to Mesopotamia, Egypt and southern Europe. Present information is inadequate to decide whether or not it is an effective breeding host of louse-flies; its semi-aquatic habits would seem to be a deterrent. However, Schuurmans Stekhoven (1923, p. 73) states definitely that, on Sumba (Indonesia), *H. variegata* occurs on water buffaloes, preferably on both sides of the neck and on the lower breast. I mentioned before a stray of the same species on a water buffalo in India. It is not impossible that this animal may be as good a host as ordinary cattle. The wild gaur, *Bibos gaurus*, of India, Indo-China and the Malay Peninsula, gave rise to a local domesticated form, the gayal, also without known hippoboscid. The banteng, *Bibos banteng* (= *B. sondaicus*), found from Burma to Indo-China, Java and Borneo, likewise has a domesticated form; no fly is known actually to breed on it; but I have seen one stray *H. equina* from a domestic banteng in Java. The common and nearly cosmopolitan domestic cattle are traced back by Antonius (1922) to at least two now extinct subspecies of wild *Bos taurus*. The short-horned types he derives from the wild *Bos taurus brachyceros,* probably domesticated in western Europe in early Neolithic times (*circa* 6000 to 8000 B. C.). The long-horn and zebu types seem to have been produced later (? late Neolithic, *circa* 5000 B. C.) from the wild urus, *Bos taurus primigenius,* which survived in Poland until early in the 17th Century A. D. The urus was at one time widespread in Europe, North Africa and Asia Minor. It was probably domesticated in the Mediterranean area, possibly in Egypt (before the Fifth Dynasty, *circa* 2500 B. C.) or Mesopotamia. Both *H. equina* and *H. variegata* are common on domesticated cattle of the *Bos taurus* types, wherever these flies are found, and they seem to make little distinction between bovines and equines. It is not certain, however, that the two species often live side by side on the same individual host. In India and Indonesia, where their ranges overlap, *H. equina* is perhaps a more recent introduction by Man than *H. variegata;* according to Schuurmans Stekhoven (1923, p. 83), the former is not as abundant at present in Indonesia as the latter.

The different areas inhabited by *H. equina* and *H. variegata* suggest that their original wild hosts may not have been the same. The origin of *H. equina* is the most difficult to determine, although this fly was presumably at first native to Europe, where it lives even now under seemingly natural conditions and survives the winter in certain localities either as puparia or on feral hosts. The original hosts could have been the wild horse, *Equus caballus,* or the wild *Bos taurus,* or both. The last of these three alternatives seems the most plausible, although it is doubtful that convincing proof can ever be forthcoming. After the introduction of domestic horses into western Asia, *H. equina* passed from them to donkeys and mules. *H. variegata,* a subtropical and tropical insect, could scarcely have originated in Europe, where, moreover, it has never been found; nor could it have lived at first on wild equines, if the European origin of the domestic horse is correct. The possibility of the wild ass, *Equus asinus,* being the original host of this fly cannot be ruled out; but the present preference for warmer areas makes it more probable that it lived originally on the urus, *Bos taurus primigenius,* in the countries along the southern shores of the Mediterranean. There is just a possibility that it may have come originally from the wild water buffalo, *Bubalus bubalis;* unfortunately nothing is known of the hippoboscids that occur on this animal in nature.

Hippobosca rufipes v. Olfers is strictly African, being limited to Tanganyika, the southern Belgian Congo (Katanga; elsewhere only as temporary introductions), Angola, Northern and Southern Rhodesia, Bechuanaland, South West Africa, Transvaal, Portuguese East Africa, Zululand, Natal, Orange Free State, and Cape Province. Its extension into Angola, Rhodesia and the southern Congo may be of very recent date and perhaps due to Man. It breeds in nature on several antelopes listed in the discussion of the Artiodactyla, and possibly also on giraffes. It is noteworthy that it has never been taken on either zebras or African buffaloes. Nowadays it is often an abundant parasite of domestic equines and cattle, which were introduced fairly recently by Man into Central and South Africa, certainly within historic times (perhaps only 5 or 6 centuries ago). There are no fully reliable records of *H. rufipes* from accidental hosts, beyond a vague mention by Bedford (1927, p. 782) that it will occasionally settle on dogs, and the possibility that the giraffe may not be a regular breeding host. v. Olfers' type of *H. rufipes* was said to have been taken by Lichtenstein on an ostrich; but the author suggested that it probably flew to this bird from a zebra. There is no reliable evidence that it was actually taken on either of these hosts, from which there is no later record. At one time I suggested (1931, p. 322) that the original wild host was one of the South African zebras; but this seems most improbable, particularly in view of the several recorded occurrences on antelopes (eland, blue wildebeest, springbok, and steinbok). Most probably the fly was at first a common parasite of some of the antelopes which even a century ago were extremely abundant in South Africa, but are now nearing extinction. From them it passed first to the cattle introduced by native tribes and later to the horses, donkeys and mules imported by Europeans.

Hippobosca camelina Leach is reported at present from Mauritania, Morocco, Algeria, Tunis, the Sahara, Libya, Cyrenaica, Egypt, Northern Nigeria, the eastern Sudan, Eritrea, Abyssinia, Somaliland, northern Kenya and adjoining sections of Uganda, Arabia, Palestine, Syria, Iraq, Iran, Turkestan, Afghanistan, and northwestern India. The record from South West Africa (Speiser, 1908*a*, p. 177) was no doubt based on a temporary introduction with camels and there is no evidence that the fly is now established there. It is more difficult to account for the single specimen reported by Massonat (1909, p. 248) from a horse of the Camargue, southern

France; I am inclined to attribute it to some error and it certainly does not warrant including the species in the French fauna.[24]

The true breeding hosts of *H. camelina* are two distinct species (not subspecies) of *Camelus: C. bactrianus,* the two-humped or Bactrian camel, and *C. dromedarius,* the one-humped dromedary. Flies are frequent on both species in domestication; but they have not been recorded from wild *C. bactrianus,* originally a Central Asiatic species, said to survive in Chinese Turkestan (Gobi Desert) and Mongolia. *C. dromedarius* is no longer known in the wild state, but is believed to have lived originally in the deserts of North Africa and Arabia. When and where these animals were domesticated is most obscure; it was certainly undertaken in different areas corresponding to the original homes of the two wild ancestors. No doubt *Hippobosca camelina* was retained from one or from both of these. I am inclined to regard it as originally a parasite of the wild *C. dromedarius* in Northeast Africa. If so, it passed later from the domesticated dromedary to the domesticated Bactrian camel; but there seems to be no way of proving this surmise. *H. camelina* does not often stray to other hosts. Although it is usually claimed to occur on horses, there are very few definite records from these animals. Massonat (1909, p. 248) says that it is found on them in Algeria and Tunis, but gives no details, and he may have made the statement from hearsay; his one fly from a horse in the Camargue, southern France, is most puzzling. Austen (1921, p. 122), however, definitely states that he found it together with *H. equina* on horses in Palestine. Of the many specimens I have seen, only one, from Cairo, Egypt, was labelled as taken on a horse (received from Dr. Efflatoun Bey). Possibly the occurrence on equines is very temporary. As shown below, this fly occasionally attacks Man also.

I discussed the distribution and host relations of *Melophagus ovinus* at some length in my Monograph of the Melophaginae (1942*a*, pp. 183–188) and it seems unnecessary to repeat the details here. I pointed out that, contrary to accepted opinion, the sheep-ked is not to be found wherever sheep are kept in domestication. Except for temporary introductions, it is absent from all hot tropical areas (being found only at high altitude within the tropics) and from many oceanic islands. In an earlier section dealing with the effect of macroclimate, I attempt to correlate this peculiarity with a predilection for low or moderate temperatures.

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[24] I have seen a male *H. camelina* labelled ''Condon, Western Australia, September 17, 1907.'' It was most probably collected on a freshly imported camel. I can find no further evidence that this fly ever became established in Australia, where camels now are feral in certain districts.

The host relations will be considered more in detail here. At present the only known effective breeding hosts of *M. ovinus* are domestic sheep and possibly domestic goats, as well as sheep gone feral. The sheep-ked is usually said to occur on goats where these animals mingle freely with sheep. It is difficult to decide how often this happens, as there are few definite observations, most authors merely repeating earlier published statements. Macquart (1847, p. 112 [96]) first mentioned finding one ked on a goat, presumably in France. Zavattari (1930, *Boll. Soc. Italiana Med. Ig. Colon.*, No. 13, Suppl., p. 9 of reprint) reports the occurrence of *M. ovinus* on both goats and sheep in Cyrenaica, and Olenev (1931, p. 37) on goats and sheep in the Irghiz District of Turkestan. Babcock and Parish (1936, *Insect Pest Survey Bull.*, **16**, No. 4, p. 146) found it on sheep and goats at Sonora, Texas. I reported (1942*a*, p. 183) a ked taken on a goat running with sheep in Lander Co., Nevada, by W. L. Jellison. According to de Buen (1950, p. 415) keds occurred on sheep and goats at Chapingo, Mexico, at 2700 meters altitude. All these records are clearly based on goats closely associated with sheep, which may supply them with all their keds. There is actually no convincing proof that the sheep-ked could reproduce continuously and therefore survive as a species on goats alone. Precise observations are needed of the possible occurrence on goats in the absence of sheep. Railliet (1888, p. 217) mentions finding the sheep-ked on a "chabin," the rather problematical hybrid of goat and sheep, brought from Chile to France.

The occurrence of *M. ovinus* on domestic cattle is exceptional. Olenev (1931, p. 37) mentions this host from the Irghiz District in Turkestan. I listed (1942*a,* p. 182) a specimen labelled as taken on a cow in Tibet; and I have since seen 4 keds collected by Dr. Bilal-Golem on a cow at Askale near Erzürum, Asiatic Turkey. Pullar (1937) reported the unusual case of a calf near Melbourne, Australia, infested with 50 to 60 adult keds and 20 to 30 puparia adhering to the hairs of the neck. I can find only one report of *M. ovinus* from a domestic horse, by Charbonnier (1912, p. 75), near Bristol, England. Olenev (1931, p. 37) states that it occurs sometimes on domestic camels in the Irghiz District, Turkestan. I find no reliable evidence for its occurrence, reported by Velu and Barotte (1924, *Eléments Pratiques Pathologie Vétérinaire Exotique,* 2nd Edition, p. 378), on the South American domesticated alpaca, *Lama glama* *pacos.* Turning now to the reports of sheep-keds on wild hosts, the following should be first discarded as erroneous: those from sick roebuck, *Capreolus capreolus,* in Switzerland, by Grieder (1938, *Schweizer Arch. f. Tierheilk.,* **80**, p. 25), based on misnamed *Lipoptena cervi;* those from the chamois, *Rupicapra rupicapra,* by Massonat (1909, p. 263) and Bornand (1936, p. 30; 1939, p. 67), based on the failure to recognize *Melophagus rupicaprinus;* and the supposed sheep-keds found by Randolph and Eads (1947, p. 600) on the Virginia deer, *Odocoileus virginianus,* in Texas, which were *Lipoptena mazamae.* Fletcher and Sen (1929, p. 51) mention a sheep-ked from a panther shot in the Central Provinces of India; but, as they did not see the specimen, the record is questionable. Wrublewski (1912, p. 384) reported finding *M. ovinus* on one of the few surviving wisents in the forest of Bialowieza, Poland. I have seen a specimen labelled as taken on a mule deer, *Odocoileus h. hemionus,* at Dayville, Oregon, by Mr. Stage-Hendricks; and I recorded (1942*a,* p. 182) keds from a wolf, *Canis lupus* subsp., in Alaska, and from a coyote, *Canis latrans,* in British Columbia. The reported attacks on Man are discussed in the sequel.

The reports of *M. ovinus* from wild sheep should be discussed in connection with the putative ancestors of domestic sheep. The latter are usually regarded as a distinct species, *Ovis aries,* not known at present in the wild state. Possibly the domesticated races all arose from a wild ancestor now extinct. More probably they had a mixed ancestry, the main stock being the wild mouflon, *Ovis musimon,* now surviving in Sardinia and Corsica, with contributions from the argali, *Ovis ammon,* of Central Asia and possibly from the urial, *Ovis orientalis,* of Asia Minor. Domestication occurred at a very early date, probably in the Neolithic (*circa* 5000 to 4000 B. C.) and presumably in Asia Minor or the islands of the Mediterranean. Hase's (1940, p. 643) statement that ''*Melophagus* lives of course also on wild sheep,'' though possibly correct, is based on very few facts, none of them fully reliable. Speiser's (1908, p. 444) record of his *M. ovinus* var. *fera* (a synonym of *M. ovinus*) from ''Steinbock'' in the Caucasus, must be disregarded since it is impossible to know what host was meant. I have seen 2 specimens of *M. ovinus* labelled as taken from a museum skin of Marco Polo sheep, *Ovis ammon polii;* but the locality or history of this skin are unknown and it may have come from an animal kept in a zoological park. Ferris and Cole (1922, p. 192) described their *M. ovinus montanus* from specimens taken by C. G. Hewitt at the Alaska-Yukon Boundary on ''mountain sheep,'' which they assumed were native American sheep (subspecies of *Ovis canadensis*). There is no certainty, however, that these keds did not come from Old World domestic sheep gone feral. If they actually did occur on American wild sheep, the animals might have acquired them from feral domestic sheep, since there are no characters separating *M. o. montanus* from the usual sheep-keds. Moreover, no other collector has ever found keds on native American sheep (see J. Bequaert, 1942*a*, pp. 187–188). A thorough investigation of the several surviving wild species and races of *Ovis* for ectoparasites is urgently needed before their last remnants become extinct. Meanwhile the original host and country of *M. ovinus* remain unsolved problems.

Lipoptena capreoli, the goat-ked, is restricted to the countries bordering the eastern Mediterranean, Asia Minor and northwestern India (Punjab). It does not occur in Egypt, Italy or farther west. Its only known breeding hosts are domestic goats and it is remarkable that it has not spread with these animals over a wider territory. Austen (1925, p. 23) reported a winged male taken on a dog in Asiatic Turkey (Dardanelles) by A. D. Fraser; the collector's note that it was "fairly common" was most likely due to a confusion with *Hippobosca longipennis.* In the same paper, Austen lists a fully winged male taken by P. A. Buxton on a horse's withers in Palestine and specimens collected by M. Sidky on camels and cow at Jerusalem. These are clearly all stray occurrences similar to those observed for other common species of *Lipoptena* in Europe and North America. They do not prove that *L. capreoli* ever feeds on these unusual hosts. Aschner (1931, p. 370) noted that it did not pass to domestic sheep in Palestine, even when they graze with infested goats. The main ancestral stock of the domestic goat, *Capra h. hircus,* is generally believed to have been the wild goat or pasang, *Capra hircus aegagrus,* which survives to this day in a few localities of the Greek Islands, Asia Minor, Turkestan, Iran, and western India. A few breeds may have been derived from the markhor, *Capra falconeri,* of Central Asia. Domestication presumably started in the late Neolithic (*circa* 5000–3500 B. C.) and possibly in the Balkan Peninsula (from a now extinct race of *C. hircus*) and Asia Minor (from *C. h. aegagrus*). It is unfortunate that *L. capreoli* has not been reported definitely from wild *C. h. aegagrus;* although there is a possibility that the supposed *L. chalcomelaena* mentioned by Speiser (1905, p. 354) from this host might have been *L. capreoli* instead. It should, moreover, be mentioned that these two species of *Lipoptena* are very closely related. It is even thinkable that *L. capreoli* was produced recently by *L. chalcomelaena,* following the domestication of the wild goat.

Summary of Known Breeding Hosts. The many details of the foregoing analysis tend to obscure the main points at issue in the host-parasite problem of the Hippoboscidae. A summary of the species of flies which, upon present evidence, definitely or presumably use the several orders of hosts for breeding purposes may be useful. When the status of the order is as yet uncertain with regard to the type of host relation involved, the specific name is followed by a query. The list brings out the outstanding importance of the Passeriformes and Falconiformes among the birds and of the Artiodactyla among the mammals, for the survival of these parasites.

I. Birds

Struthioniformes (1) : *Hippobosca struthionis.*

Tinamiformes (2) : *Microlynchia crypturelli* (?) ; *Stilbometopa podopostyla.*

Procellariiformes (1) : *Olfersia aenescens* (?).

Pelecaniformes (5) : *Olfersia aenescens; O. spinifera; O. fossulata; O. sordida; Lynchia schoutedeni.*

Ciconiiformes (2) : *Lynchia albipennis; Ornithoica confluenta.*

Falconiformes (16) : *Olfersia bisulcata; O. fumipennis; Lynchia angustifrons; L. nigra; L. wolcotti; L. dukei; L. americana; Pseudolynchia canariensis; Ornitheza metallica* (?) ; *Ornithoctona erythrocephala; O. plicata; Ornithomyia avicularia* (?) ; *O. fringillina* (?) ; *O. perfuga* (?) ; *Ornithoica pusilla; O. turdi.*

Galliformes (9) : *Olfersia coriacea; Lynchia hirsuta; L. americana; L.* (*Ornithophila*) *maquilingensis; Microlynchia pusilla; Stilbometopa impressa; Ornithomyia fringillina* (= *lagopodis*) ; *Ornithoctona erythrocephala* (?) ; *O. plicata* (?).

Gruiformes (3) : *Lynchia holoptera; L. pilosa; Ornithomyia remota.*

Charadriiformes (2) : *Olfersia aenescens* (?) ; *O. fossulata* (?).

Columbiformes (8) : *Pseudolynchia canariensis; Microlynchia pusilla; Ornithoctona erythrocephala; O. plicata; O. australasiae* (?) ; *Stilbometopa podopostyla; S. fulvifrons; Ornithoica pusilla.*

Psittaciformes (5) : *Ornitheza metallica; Ornithomyia avicularia; Ornithoctona erythrocephala* (?) ; *O. plicata* (?) ; *Ornithoica vicina.*

Cuculiformes (3) : *Microlynchia pusilla; Pseudolynchia canariensis* (?) ; *Ornithoica turdi.*

Strigiformes (11): *Lynchia fusca; L. americana; Pseudolynchia rufipes; Ornithomyia fringillina* (?); *O. avicularia; O. perfuga* (?); *Ornithoctona erythrocephala* (?); *O. plicata* (?); *Ornithoica vicina; O. turdi* (?); *O. pusilla* (?).

Caprimulgiformes (3): *Pseudolynchia brunnea; P. rufipes; Ornithomyia perfuga* (?).

Apodiformes (9): *Crataerina pallida; C. melbae; C. longipennis; C. propinqua; C. acutipennis; Myiophthiria reduvioides; M. lygaeoides; M.* (*Brachypteromyia*) *fimbriata; M.* (*B.*) *neotropica.*

Trogoniformes (1): *Ornithoctona* (*Ornithopertha*) *nitens.*

Coraciiformes (6): *Ornitheza metallica; Ornithomyia perfuga* (?); *Ornithoctona plicata* (?); *Ornithoica pusilla; O. unicolor; O. turdi.*

Piciformes (2): *Ornithomyia fringillina* (?); *Ornithoica vicina* (?).

Passeriformes (17): *Ornithomyia avicularia; O. fringillina; O. remota; O. biloba; O. comosa; O. fur; O.* (*Pseudornithomyia*) *ambigua; Ornithoctona laticornis* (= *O. platycera*); *O. plicata; O. fusciventris; Stenepteryx hirundinis; Crataerina seguyi; Ornitheza metallica; Microlynchia pusilla* (?); *Ornithoica turdi; O. vicina; O. pusilla.*

II. Mammals

Marsupialia (3): *Ortholfersia phaneroneura; O. macleayi;* (?*O. tasmanica* and *O. raveni,* doubtfully distinct from the preceding two); *Austrolfersia ferrisi.*

Primates (1): *Allobosca crassipes.*

Carnivora (1): *Hippobosca longipennis.*

Perissodactyla (3): [*Hippobosca equina; H. variegata; H. rufipes;* on domestic hosts only].

Artiodactyla (27): [*Hippobosca equina; H. variegata; H. camelina; Melophagus ovinus; Lipoptena capreoli;* on domestic hosts only]. *Hippobosca rufipes; H. fulva; H. hirsuta; Lipoptena cervi; L. depressa; L. mazamae; L. guimarãesi; L. efovea; L. japonica; L. gracilis; L. rusaecola; L. moschi* (?); *L. hopkinsi; L. antilopes* (?); *L. couturieri; L. pauciseta; L. chalcomelaena; Neolipoptena ferrisi; Echestypus sepiaceus; E. paradoxus; E. binoculus; Melophagus rupicaprinus.*

Type and Degree of Specificity. Even the preceding summary of the orders acting as effective breeding hosts of the several flies may leave the impression that the Hippoboscidae have little or no host specificity. It is now my purpose to show that such a conclusion would be too sweeping, but that the specificity of these flies is of a peculiar type, differing markedly from that of most other ectoparasites.

Needless to say, the many occasional or accidental host occurrences, as well as the flies recorded only from one or two hosts, will be disregarded in what is to follow. It seems also advisable not to consider further the 5 species parasitic of domestic mammals which are not known at present to breed on surviving wild hosts. Their original hosts and habitats are uncertain and it is difficult to account for their present erratic distribution, which rarely covers the same area as that of the normal domestic hosts. It is generally recognized that domestic animals live under highly artificial conditions, so that the domestication of the hosts may have influenced indirectly their ectoparasites also. As a result, the host relations may be no longer strictly comparable to those of ectoparasites of wild hosts in a natural environment. Nevertheless, the general pattern of the host preference of these flies does not differ essentially from that of other hippoboscids, particularly those found on wild mammals. *Hippobosca equina* and *H. variegata* breed on both Perissodactyla (equines) and Artiodactyla (bovines); *H. camelina* breeds only on Artiodactyla (Tylopoda or Camelidae); and *Melophagus ovinus* and *Lipoptena capreoli* only on Artiodactyla of the subfamily Caprinae.

For the more common flies with many reliable records, I mention briefly the frequency on some of the hosts. This illustrates the type of quantitative evidence which may be used to determine the effective or true breeding hosts of each fly. The species may be arranged conveniently in four main groups on the basis of a gradually widening range of hosts or decreasing host specificity.

A. Flies restricted to one or to a few closely related species belonging to one genus (monoxenous hippoboscids).[25]

Hippobosca struthionis. Specific of the one Recent species of ostrich, *Struthio camelus,* the sole surviving member of the Struthionidae and of the Order Struthioniformes. It has now been taken on two of the 6 subspecies recognized by Peters (1931): *S. c. massaicus* and *S. c. australis.* It would be of great interest to establish its presence or absence on the other subspecies.

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[25] The terms monoxenous, oligoxenous, pleioxenous and polyxenous here adopted for the several degrees of specificity, are purely descriptive, no idea of causality being implied. For this reason I prefer them to be more familiar monophagous, oligophagous, pleiophagous and polyphagous (Eichler, 1952, p. 228), which stress the food preferences of the parasites. The host selectivity of the Hippoboscidae, at any rate, is determined only in part by the food; several other factors are equally important.

Olfersia spinifera. Specific of the genus *Fregata,* which forms by itself the family Fregatidae in the Order Pelecaniformes. Peters (1931) recognizes 5 species and a total of 14 subspecies. The fly is known from 3 of the species: *F. aquila, F. magnificens* (on 2 of the 3 subsp.), and *F. minor* (on 2 of the 6 subsp.). It may be expected to occur on all members of the genus.

Olfersia fumipennis. Specific of the genus *Pandion,* which forms by itself the family Pandionidae, in the Order Falconiformes, and consists of a single species with 5 subspecies (Peters, 1931), 4 of them known as hosts.

Stenepteryx hirundinis. A specific parasite of *Delichon urbica,* in the Hirundinidae of the Order Passeriformes. Probably only a straggler on *Hirundo rustica, Riparia riparia* (one fly from Suffolk, England, collected by R. Meinertzhagen), *Riparia rupestris,* and *Apus apus;* although the matter is by no means settled. (See Thompson, 1947*b,* p. 269).

The Old World species of *Crataerina, C. pallida, C. melbae, C. longipennis, C. propinqua,* and *C. acutipennis,* are, so far as known, strictly specific of the genus *Apus,* in the Apodidae of the Order Apodiformes. They are recorded from 9 of the 15 species recognized by Peters (1940): *A. apus, A. melba, A. aequatorialis, A. pallidus, A. unicolor, A. horus, A. affinis, A. caffer,* and *A. pacificus. C. melbae* seems to be restricted to *A. melba;* but most of the other flies probably occur on more than one species of swifts; *C. acutipennis,* for instance, is known from seven. Straying to other hosts, such as swallows (Hirundinidae), is very rare. It is rather surprising, therefore, that the only New World species, *Crataerina seguyi,* lives exclusively on swallows, not on swifts.

Myiophthiria reduvioides. Strictly specific of the genus *Collocalia,* in the Apodidae of the Order Apodiformes, being known from 3 species.

Myiophthiria lygaeoides. Known thus far from only one species of *Collocalia,* in the Apodidae of the Order Apodiformes.

Myiophthiria (*Brachypteromyia*) *neotropica.* No doubt restricted to the Apodidae in the Order Apodiformes and known only from one species of *Aëronautes.*

Ornithomyia biloba. I regard this as a specific parasite of

Hirundo rustica and possibly other species of *Hirundo*. The few reliable reported occurrences on *Delichon* and *Riparia* are almost certainly due to straggling. In any case, the fly is restricted to the Hirundinidae in the Order Passeriformes. Some other closely related species of *Ornithomyia* for which a fair number of host records are available, such as *O. comosa* and *O. fur,* are not so strict in their choice, occurring on several genera of Hirundinidae. However, the taxonomy of these flies is confused. Possibly *O. fur* and *O. biloba* are not specifically distinct, in which case the species will have to be transferred to the next group of flies.

Ortholfersia. There are probably only two, not four, valid species in this genus, but their correct names cannot be defined at present. In any case, these flies are strictly specific of the family Macropodidae in the Order Marsupialia and are definitely known only from 2 species of *Protemnodon.*

Austrolfersia ferrisi (= *Ortholfersia tasmanica* Ferris, not of Wesché). Strictly specific of the Macropodidae in the Order Marsupialia and known only at present from one species of *Thylogale.*

Lipoptena pauciseta. A specific parasite of the genus *Muntiacus* in the Cervidae of the Order Artiodactyla. It is known thus far only from one of the 5 species, *Muntiacus muntjak* (on 3 of the 8 subspecies).

Lipoptena rusaecola. A specific parasite of *Cervus* (*Rusa*) *unicolor* in the Cervidae of the Order Artiodactyla, and known only from the Philippine race, *C. unicolor philippinus;* it may be expected to occur also on some of the other subspecies.

Lipoptena depressa. Strictly specific of Cervidae in the Order Artiodactyla. Definitely known only from 2 species of *Odocoileus.* That it breeds regularly on *Cervus canadensis* needs confirmation.

Lipoptena japonica. Known only from *Capricornis crispus,* in the Bovidae (Order Artiodactyla).

Lipoptena couturieri. Specific of the European chamois, *Rupicapra rupicapra,* in the Bovidae (Order Artiodactyla).

Lipoptena chalcomelaena. Known at present from *Capra* only (family Bovidae, Order Artiodactyla); and more specifically from 2 subspecies of *Capra ibex.*

Lipoptena guimarãesi. This recently discovered species is a specific parasite of the South American *Ozotoceros bezoarticus,* in the Cervidae (Order Artiodactyla).

Lipoptena gracilis. A strictly specific parasite of *Tragulus,* in the Tragulidae (Order Artiodactyla). It has now been taken on 7 subspecies of *T. javanicus* (= *kanchil*); most probably it occurs on some of the remaining subspecies also. It should be looked for on the other 3 species of the genus.

The foregoing 24 species, 13 from birds and 11 from mammals, may be regarded as strictly host-specific, being limited for breeding purposes either to one species (in 15 cases) or to one genus (in 9 cases). It is doubtful, however, that the restriction always implies an active or keen host preference. Sometimes it is fortuitous, the host belonging to a monotypic genus (*Delichon, Rupicapra, Ozotoceros*) or even being the only species of its family (*Struthio, Pandion*). The remaining one-host flies, from *Thylogale, Muntiacus, Capricornis, Cervus, Capra, Tragulus, Collocalia,* and *Aëronautes,* have not been sufficiently collected. Probably some of them will eventually be found on other species of the same genus or may even have to be transferred to the next group.

B. Flies restricted to members of several closely related genera belonging to one family (oligoxenous hippoboscids).

Olfersia bisulcata. Restricted to the Cathartidae in the Order Falconiformes and known from 5 species in 4 of the 5 genera of the family. It may be expected to be taken eventually on the fifth (*Gymnogyps*) also.

Lynchia hirsuta. Restricted to the Phasianidae in the Order Galliformes and known from 4 species in 3 genera. The fly is very common on *Lophortyx* in certain sections of California.

Lynchia holoptera. Restricted to the Rallidae in the Order Gruiformes; known from 3 species in 3 genera.

Lynchia pilosa. Probably specific of the Otitidae in the Order Gruiformes, being known from 4 species in 4 genera of this family. Two records from Pteroclidae in the Order Columbiformes are at present regarded as stray occurrences.

Lynchia (*Ornithophila*) *maquilingensis* (possibly not separable from *L.* [*O.*] *simplex*). Apparently a specific parasite of wild Phasianidae in the Order Galliformes, in the Indo-Malayan Region; definitely known from 2 species in 2 genera.

Lynchia schoutedeni. Probably specific of the Phalacrocoracidae in the Order Pelecaniformes; known from 3 species in 3 genera.

Pseudolynchia brunnea. Restricted to the Caprimulgidae in the Order Caprimulgiformes; on 6 species in 5 genera. Of 23 verified individual records, 22 were from Caprimulgidae and one from a thrush.

Stilbometopa impressa. Restricted to the Phasianidae in the Order Galliformes; on 3 species in 2 genera. Very abundant on these birds in the western United States; there are only 2 stray records, one from the domestic fowl, the other from a hawk.

Ornithoctona (*Ornithopertha*) *nitens.* Appears to be specific of the Trogonidae, sole family in the Order Trogoniformes, being known from 4 species in 2 genera. The case calls for further study.

Crataerina seguyi. Restricted to the Hirundinidae in the Order Passeriformes, being known from 3 species in 2 genera.

Myiophthiria (*Brachypteromyia*) *fimbriata.* Restricted to the Apodidae in the Order Apodiformes; on 2 species in 2 genera.

Ornithomyia (*Pseudornithomyia*) *ambigua.* Specific of the Hirundinidae in the Order Passeriformes, in tropical America, where it is known from 4 species in 4 genera. A new related species of the same subgenus probably has the same host preference.

Ornithoica confluenta (= *O. beccariina*). Restricted to the Ardeidae in the Order Ciconiiformes and known thus far from 4 species in 4 genera.

Ornithoica unicolor. Most probably a specific parasite of the Bucerotidae of the Order Coraciiformes, but recorded only from 3 species in 3 genera. Further observations are needed in this case.

Lipoptena cervi. Restricted to the Cervidae in the Order Artiodactyla. It is definitely known to breed on 5 species in 4 genera.

Lipoptena efovea. Restricted to the Cervidae in the Order Artiodactyla. The few available records are from 2 species in 2 genera.

Lipoptena mazamae. Restricted to the Cervidae in the Order Artiodactyla and known from 6 subspecies of one species of *Odocoileus* and from 3 species of *Mazama.*

Lipoptena hopkinsi. Restricted to antelopes in the Bovidae of the Order Artiodactyla and reported from 4 species in 3 genera.

Echestypus paradoxus. A specific parasite of antelopes in the Bovidae of the Order Artiodactyla. Known from 9 species in 6 genera.

Echestypus sepiaceus. A specific parasite of antelopes in the Bovidae of the Order Artiodactyla. Known from 9 species in 5 genera.

Echestypus binoculus. A specific parasite of antelopes in the Bovidae of the Order Artiodactyla. Known from 2 species in 2 genera.

Melophagus rupicaprinus. Known at present to breed on 2 species of Bovidae in the Order Artiodactyla, both of the subfamily Caprinae: *Rupicapra rupicapra* and *Capra ibex ibex.*

Hippobosca hirsuta. A specific parasite of antelopes in the Bovidae of the Order Artiodactyla. Known from 3 species in 2 genera.

Hippobosca fulva. A specific parasite of antelopes in the Bovidae of the Order Artiodactyla. Known from 3 species in 3 genera.

The true host status of some of the African antelopes reported for *L. hopkinsi, E. paradoxus, E. sepiaceus, E. binoculus, H. hirsuta,* and *H. fulva* is questionable. Available records are far too few and too uncritical. Several of these animals may be only accidental hosts, so that the flies are possibly more narrowly host-specific than now appears.

As matters now stand, 24 species, 14 from birds and 10 from mammals, are generally found breeding on a variety of hosts within a single family.

C. Flies breeding on a fair number of representatives of two or exceptionally more families within one order (pleioxenous hippoboscids).

Olfersia sordida. Restricted to the Pelecaniformes, where it breeds on 2 species in one genus of the Phalacrocoracidae and on one species in one genus of the Pelecanidae. Of 15 verified individual records, 3 are from *Phalacrocorax,* 11 from *Pelecanus,* and one from a wader (*Leucophoyx*).

Olfersia coriacea. A specific parasite of the Cracidae in the Order Galliformes. Known from 6 species in 3 genera and possibly breeding also on one species in one genus of the Meleagridae.

Lynchia albipennis (= *ardeae*). A cosmopolitan fly decidedly specific of the Order Ciconiiformes. Known from 27 species in 16 genera of the Ardeidae, 3 species in 3 genera of the Threskiornithidae, and 2 species in 2 genera of the Ciconiidae. Although there are also several records from Gruiformes (in 3 genera of the Rallidae) and Charadriiformes (in 4 genera), it is extremely doubtful that these birds are effective breeding hosts in the absence of true waders. In the New World, for instance, of 101 individual host records verified by myself, 88 are from 22 species in 17 genera of Ciconiiformes; the remaining 13 are scattered mostly among the Gruiformes (4 from 3 species in 3 genera), Charadriiformes (3 from 2 species in 2 genera), and Falconiformes (3 from 3 species in 3 genera), with 1 record each for the Anseriformes, Strigiformes and Passeriformes.

Lynchia angustifrons. Decidedly specific of the Order Falconiformes, being known from 4 species in 4 genera of the Falconidae, 12 species in 8 genera of the Accipitridae, and 1 species of the Cathartidae. Of a total of 41 verified individual records, 26 are from diurnal raptores, while the remaining 15 are scattered among the Strigiformes (4), Trogoniformes (1), Coraciiformes (2), Piciformes (4), and Passeriformes (4).

Lynchia nigra. Highly specific of the Order Falconiformes. Known from 9 species in 4 genera of the Falconidae, 13 species in 8 genera of the Accipitridae, and 1 species of the Cathartidae. Of 44 verified individual records, 42 are from diurnal raptores and only one each from Cuculiformes and Strigiformes.

Lynchia wolcotti. Although this species has been little collected, it is most probably specific of the Falconiformes, since of 8 verified individual records 6 are from 3 species in 3 genera of the Accipitridae and only 2 from Strigiformes.

Lynchia dukei. Strictly specific of the Falconiformes, the 19 verified host records being from 8 species in 8 genera of the Accipitridae; 7 of these are from the fishing eagle, *Haliaeëtus vocifer.*

Lynchia fusca. In sharp contrast to the foregoing four species, this fly is specific of the Strigiformes, having been taken on 14 species in 11 genera of the Strigidae. Of 88 verified individual records, 78 are from owls, 7 of the remainder from Falconiformes (5 species in 4 genera), 2 from Columbiformes, and one from Charadriiformes. There are 26 records from 5 races of *Bubo virginianus* and 20 records from 7 races of *Otus asio.*

Ornithoctona laticornis (=*platycera*). This is probably the most common bird-fly in Africa. There are now records, mostly verified by myself, from 43 species of birds of 7 orders. The individual records are overwhelmingly from Passeriformes, which unquestionably furnish the only true breeding hosts. Within this order, however, little further preference is shown, the total of 37 parasitized species being divided among the families as follows: Hirundinidae, 2 in 2 genera; Muscicapidae, 13 in 10 genera; Laniidae, 6 in 5 genera; Zosteropidae, 1; Fringillidae, 3 in 3 genera; Ploceidae, 7 in 5 genera; Sturnidae, 3 in 3 genera; Oriolidae, 1; and Dicruridae, 1. The remaining stray hosts are scattered among the Ciconiiformes (1 species of Phoenicopteridae), Anseriformes (1 species of Anatidae), Columbiformes (1 species of Columbidae), Trogoniformes (1 species of Trogonidae), Coraciiformes (1 species of Alcedinidae), and Piciformes (1 species of Picidae).

Ornithoctona fusciventris. This American fly is particularly common in the tropics. There are records from 41 species of 4 orders, but almost all (37) are Passeriformes (11 Thraupidae; 9

Muscicapidae; 4 Fringillidae; 3 Formicariidae; 3 Tyrannidae; 4 Furnariidae; 1 Vireonidae; 1 Rhinocryptidae; 1 Icteridae; and 1 Corvidae). The remaining 4 hosts belong to the Falconiformes (2 Accipitridae), Galliformes (one in Cracidae), and Coraciiformes (one in Momotidae). The individual records favor the Passeriformes even more overwhelmingly as breeding hosts, since 49 of the 54 I verified are from passerines. The predilection is particularly marked for the Thraupidae (12 verified records), Fringillidae (10 verified records), and Muscicapidae (11 verified records).

Allobosca crassipes. Strictly specific of Madagascan lemurs, Simpson's ''Infraorder Lemuriformes'' of the Order Primates. There are reliable records from 3 species in 2 genera of the Lemuridae and from 3 species in 2 genera of the Indriidae. The parasite is probably more widespread among these two families.

Hippobosca longipennis. The wild breeding hosts of the dog louse-fly are all Carnivora; but otherwise the specificity is not pronounced, since there are reliable records from 4 species in 2 genera of Canidae, 1 species of Viverridae, 2 species in 2 genera of Hyaenidae and 4 species in 3 genera of Felidae. However, present information is inadequate to decide which of these reported hosts are effective for the survival of the species. I suspect that some of them are infested only accidentally.

Hippobosca rufipes. The wild hosts of this fly are imperfectly known, though they are all Artiodactyla. The records are chiefly from 4 species in 4 genera of antelopes (Bovidae). There is one record from a species of *Giraffa* (Giraffidae), which calls for corroboration. Possibly the species may have to be included in Group B.

Neolipoptena ferrisi. Restricted to Artiodactyla. Most host records are from 2 species of *Odocoileus* in the family Cervidae. The fly has, however, been taken on two occasions on *Antilocapra,* of the family Antilocapridae, but in so few specimens that the status of the animal as a breeding host is questionable. Possibly *N. ferrisi* should be transferred to Group A.

There is a possibility that some of the flies I have included in Group C are more narrowly host-specific than recognized. At present, 14 species, 10 from birds and 4 from mammals, seem to breed on members of more than one family in the same order.

D. Flies apparently with equally effective breeding hosts in two or more orders (polyxenous hippoboscids).

Olfersia aenescens. Breeding hosts are definitely known in the Pelecaniformes and belong to 2 species of *Phaëthon* in the Phaëthontidae and to 4 species of *Sula* in the Sulidae. However, the fly has also been taken on Procellariiformes (on one species of *Diomedea* in the Diomedeidae and on 2 species of *Puffinus* and *Pterodroma* in the Procellariidae), as well as on Charadriiformes (on 2 species of *Anous* and *Sterna* in the Laridae). As birds of these three orders usually nest promiscuously in populous rookeries, it is at present impossible to state definitely that the Procellariiformes and Charadriiformes could serve as effective breeding hosts in the absence of Pelecaniformes.

Olfersia fossulata. This fly presents much the same problem as the foregoing. It is definitely known to breed on Pelecaniformes (2 species of *Phalacrocorax* in the Phalacrocoracidae, 2 of *Sula* in the Sulidae, and 1 of *Pelecanus* in the Pelecanidae). In addition, it is taken occasionally on 2 species of Laridae in the Order Charadriiformes (*Larus belcheri* and *Larosterna inca*), marine birds which roost and breed in the same places as the Pelecaniformes, so that the host-parasite relations are again open to question.

Lynchia americana. This common North American fly is one of the least selective in the matter of hosts. It breeds regularly on a variety of species and genera in 3 orders: in the Falconiformes on 2 species in one genus of Falconidae and 10 species in 5 genera of Accipitridae; in the Strigiformes on 6 species in 6 genera of Strigidae; in the Galliformes on 3 species in 3 genera of Phasianidae and on one species of Meleagridae. Of 286 verified individual records, 102 are from Falconiformes (including a straggler on Pandionidae), 131 from Strigiformes and 46 from Galliformes; the remainder are scattered among the Ciconiiformes (1), Charadriiformes (1), Piciformes (1), and Passeriformes (4).

Pseudolynchia canariensis. The widespread fly of domestic pigeons is known from wild hosts in the Old World only, where it breeds on at least 2 orders: in the Falconiformes on 11 species in 9 genera of Accipitridae and 6 species in 2 genera of Falconidae; and in the Columbiformes on 12 species in 4 genera of Columbidae and on 2 species in one genus of Pteroclidae. There is a possibility that some of the Cuculiformes may also be effective breeding hosts, since it has been taken on 2 species in 2 genera of Cuculidae and on 3 species in one genus of Musophagidae. The records from other orders are so few that they are clearly based on stragglers: 3 in Strigiformes and one in Coraciiformes.

Pseudolynchia rufipes. The available records seem to indicate that it breeds on birds of two orders, the Strigiformes (5 species in 4 genera of Strigidae) and the Caprimulgiformes (6 species in 4 genera of Caprimulgidae). The stray records are scattered among the Falconiformes (1 species of Accipitridae), Cuculiformes (1 species of Cuculidae), Charadriiformes (1 species of Burhinidae), Apodiformes (1 species of Apodidae), and Passeriformes (1 species each of Hirundinidae and Corvidae).

Microlynchia pusilla. Probably a fairly common fly, particularly in the American tropics, but as yet little collected because it lives often on fairly large birds where it is overlooked owing to its small size. The records suffice, however, to show that it breeds on birds of at least 3 or possibly 4 orders. In the United States it is known from 19 species of birds: of 50 verified individual records, 15 are from Columbiformes (on 4 native species of Columbidae and on the domestic pigeon), 9 from Galliformes (on 3 species of Phasianidae), and 8 from Cuculiformes (all on the roadrunner, *Geococcyx californianus,* which has no other known bird-fly); in addition 17 records are from 9 species of Passeriformes, which may or may not be true breeding hosts, and one is from a species of Caprimulgidae (Caprimulgiformes). For the remainder of the New World there are records from 15 species of birds, mostly based on isolated finds; of the 15 verified individual records, 11 are from 8 species of Columbidae (Columbiformes), the other 4 being divided among the Tinamiformes, Falconiformes, Galliformes and Passeriformes.

Ornitheza metallica. Widely distributed and common throughout the Old World tropics and subtropics, but only taken occasionally in Europe. It is known at present from 63 species of birds, usually by single individual records, so that the data are hardly adequate for our purpose. Nevertheless, it is fairly clear that the breeding hosts belong to at least 2 and possibly 3 orders. There are records from 26 species in 25 genera of Passeriformes (6 of Sturnidae, 4 of Corvidae, 4 of Muscicapidae, 3 of Fringillidae, and one each of Pittidae, Alaudidae, Hirundinidae, Pycnonotidae, Laniidae, Meliphagidae, Oriolidae, Dicruridae, and Ploceidae); and from 11 species in 5 genera of Coraciiformes (2 of Coraciidae, 1 of Upupidae, 3 of Meropidae, and 5 of Alcedinidae); these two orders certainly contain true breeding hosts. In the Falconiformes, the fly is reported from 6 species in 5 genera of Accipitridae, but their significance for effective breeding is as yet undecided. The few reports from other orders are presumably based on stragglers: 1 for Ciconiiformes (Ardeidae), 3 for Galliformes (Phasianidae and Megapodiidae), 2 for Columbiformes (Columbidae), 1 for Psittaciformes (Psittacidae), 2 for Cuculiformes (Cuculidae and Musophagidae), 2 for Strigiformes (Strigidae), 2 for Apodiformes (Apodidae), 1 for

Coliiformes (Coliidae), 1 for Trogoniformes (Trogonidae), and 5 for Piciformes (Picidae and Capitonidae).

Ornithomyia fringillina. This most common bird-fly in the Temperate Zone of the Northern Hemisphere occurs on many birds of different orders. Not all of them are effective breeding hosts, however. In North America, there are records from 104 species (3 introduced) of 7 orders. The Passeriformes unquestionably contain the majority of the true breeding hosts. Of 312 verified individual records, 257 are from 78 species of passerines (including 5 records from 3 introduced species), distributed among the following families: Tyrannidae (1 record), Muscicapidae (79 records from 28 species), Laniidae (1 record), Sittidae (3 records from 1 species), Paridae (8 records from 4 species), Thraupidae (1 record), Fringillidae (104 records from 25 species), Icteridae (28 records from 6 species), Ploceidae (2 records from one introduced species), Sturnidae (3 records from 2 introduced species), and Corvidae (7 records from 4 species). The listing of the records by species, in the taxonomic Part II of the paper, shows that the fly prefers decidedly certain genera or species and possibly occurs only as a stray on others: *Melospiza* has 36 records on 3 species (26 on *M. melodia*), *Zonotrichia* 25 on 3 species (7 on *Z. albicollis*), *Turdus migratorius* 20, *Hylocichla* 16 on 4 species (6 on *H. fuscescens*), *Spizella* 15 on 2 species, *Junco* 13 on 3 species (8 on *J. hyemalis*), *Molothrus ater* 12, *Pipilo* 8 on 3 species (6 on *P. erythrophthalmus*), *Dumetella carolinensis* 7, and *Toxostoma rufum* 7. As many as 20 genera have only one verified record and for 3 others there are single published reports which I was not able to verify; presumably most of these isolated occurrences were accidental. There are also a fair number of individual records from 3 other orders: 10 from 7 species of Falconiformes (3 for 3 species of Accipitridae, 2 for 2 of Falconidae, 1 for Pandionidae, and 1 for Cathartidae); 21 from 6 species of Galliformes (all Phasianidae); 6 from 4 species of Strigiformes (all Strigidae); and 15 from 6 species of Piciformes (all Picidae). The occurrences on the Falconiformes and Strigiformes are too few and too sporadic to have much significance; they may be all due to accidental straying from infested passerines caught by these birds. The Galliformes and Piciformes, however, most probably furnish on occasion effective breeding hosts; although the woodpeckers conceivably become infested temporarily by nesting in holes previously occupied by passerines, which might account also for some of the occurrences in owls. The 3 remaining individual records, one each on a gull (*Larus*), a woodcock (*Philohela*), and a kingfisher (*Megaceryle*), are either fortuitous or contaminations. In the Old World, this fly occurs over most of the Palearctic Region, but with as yet few records from the Mediterranean area and Asia. Precise knowledge of the host-parasite relation is restricted there mainly to information gathered during the past decade. Previously, *O. fringillina, O. avicularia* and *O. biloba* were generally confused, so that the earlier records can not be trusted.[26] In recent years, however, interest in the hippoboscids has been so keen, that a sizeable list of reliable European hosts of *O. fringillina* can now be compiled. Including a few unpublished records, as well as those reported for *O. lagopodis,* it adds up to 73 species (1 introduced) of 8 orders, only 4 species duplicating North American hosts. The species are distributed among the orders as follows: 39 Passeriformes (16 Muscicapidae, 6 Fringillidae, 5 Motacillidae, 3 Corvidae, 2 Hirundinidae, 2 Paridae, and one each of Sturnidae, Certhiidae, Prunellidae, Alaudidae, and Sittidae); 12 Charadriiformes (10 Charadriidae, 1 Haematopodidae, and 1 Laridae); 7 Galliformes (Phasianidae); 6 Strigiformes (Strigidae); 6 Falconiformes (2 Falconidae and 4 Accipitridae); 1 Cuculiformis (Cuculidae); 1 Piciformis (Picidae); and 1 Apodiformis (Apodidae). To judge from the available information on the frequency of infestations in Europe, both the Passeriformes and Galliformes contain true breeding hosts. It is doubtful whether any of the Falconiformes and Strigiformes serve as such; the captures on the remaining 3 orders are clearly accidental strays.

For the benefit of those who wish to regard *O. lagopodis* as specifically distinct, this name has been used for the following records from the British Isles by Sharp (1907), Shipley (1909), Evans (1909), Austen (1932), Moon (1939), Smart (1939, in Edwards *et al.*), Parmenter (1940), O'Mahony (1940; 1949), and Ash (1950; 1952): 3 species of Galliformes (*Lyrurus* and *Lagopus,* in the Phasianidae); 7 of Charadriiformes (*Tringa, Numenius, Vanellus, Capella* and *Pluvialis,* in the Charadriidae; *Haematopus* in the Haematopodidae; *Stercorarius,* in the Stercorariidae); 2 of Falconiformes (*Falco,* in the Falconidae; *Circus,* in the Accipitridae); 1 of Strigiformes (*Strix,* in the Strigidae); and 7 of Passeriformes (*Passer,* in the Ploceidae; *Turdus* and *Oenanthe,* in the Muscicapidae; *Sturnus,* in the Sturnidae; *Corvus,* in the Corvidae; *Anthus,* in the Motacillidae). In addition Lindroth (1931, p. 332) reported *O. lagopodis* from Iceland; and Duffield (1937, p. 166) from Norway on *Luscinia suecica.* Smart (1939) refers most of the small English *Ornithomyia* to *O. lagopodis* and considers that *O. fringillina* is rare in the British Isles, as he recognized it only from the swallow, *Hirundo rustica,* robin, *Erithacus rubecula,* and hedge-sparrow, *Prunella modularis occidentalis.*

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[26] The list of European hosts compiled by Johnsen (1948, pp. 292–295) is unreliable, since it includes records of the older authors who confused the three species.

Ornithomyia avicularia. The study of the host relations of this fly also is handicapped by the confused taxonomy of *Ornithomyia,* so that the records by earlier writers must be used with caution. The true *O. avicularia* is restricted to the Old World, where it is widely distributed over most of Europe, Asia and Africa, and extends to the Australian area. The host range likewise is considerable and the fly clearly breeds on many species of several orders; but the precise details cannot be worked out at present. In Europe, according to reliable recent records by Thompson, Smart, Ash, O'Mahony and Johnsen, and my own unpublished information, *O. avicularia* has been taken on 52 species (1 introduced) of 10 orders. The Passeriformes head the list with 23 species: 2 Paridae, 7 Muscicapidae, 3 Fringillidae, 5 Corvidae, and 1 each in the Sturnidae, Motacillidae, Prunellidae, Laniidae, Hirundinidae, and Sittidae. Probably they comprise the only effective or regular breeding hosts. The remaining hosts are scattered among the Falconiformes (7: 4 Falconidae and 3 Accipitridae), Galliformes (5 Phasianidae), Columbiformes (4 Columbidae), Strigiformes (4 Strigidae), Charadriiformes (2 Charadriidae), Gruiformes (2 Rallidae), Piciformes (2 Picidae), Ciconiiformes (1 Ardeidae), and Cuculiformes (1 Cuculidae). My records from tropical Africa (on *Necrosyrtes* in the Falconidae; and on *Corvultur* in the Corvidae) and tropical Asia (on *Otus* in the Strigidae; on *Harpactes* in the Trogonidae; on *Kitta* in the Corvidae; and on *Elachura* in the Muscicapidae) are too few to be of significance. I have seen, however, over 50 specimens from the Australian area, where the species seems to be as common as in Europe and to have also a wide host range. Most records there are from Psittaciformes (5 species of Psittacidae), Strigiformes (2 species of Strigidae), and Passeriformes (2 species of Meliphagidae and one each of Corvidae, Cracticidae and Muscicapidae), orders which certainly contain true breeding hosts; a few are from Falconiformes (one species of Accipitridae) and Caprimulgiformes (one species of Caprimulgidae).

Ornithomyia remota. Although few in number, the records of this strictly South American fly make it fairly certain that it breeds normally on some of the Gruiformes (2 species of flightless Rallidae in Tristan da Cunha) and Passeriformes (12 species; 16 verified individual records from 2 species of Tyrannidae, 1 of Furnariidae, 5 of Fringillidae, 2 of Muscicapidae, and 1 of Icteridae). In contrast, there is only one record from the Strigidae and one from the Picidae.

Ornithomyia perfuga. Restricted to Australia, where it appears to be as common as *O. avicularia,* with much the same host choice. I have seen over 60 specimens, most of them unfortunately without hosts. Records are available for 10 species of 7 orders: 2 Falconiformes (one each of Falconidae and Accipitridae), one Passeriformis (Ptilonorhynchidae), 2 Strigiformes (Strigidae), one Psittaciformis (Psittacidae), one Columbiformis (Columbidae), one Coraciiformis (Alcedinidae), and one Caprimulgiformis (Podargidae). Of these the Strigiformes (*Ninox*), Coraciiformis (*Dacelo n. novaeguineae,* the laughing jackass) and Caprimulgiformis (*Podargus strigoides,* the frogmouth) are almost certainly true breeding hosts.

Ornithoctona erythrocephala. This strictly American fly, very common in the tropics, extends northward to southern Canada. It has been taken on 93 species of 14 orders; the majority are Falconiformes (30: 5 Falconidae, 24 Accipitridae, and one of Pandionidae) and Columbiformes (20 Columbidae). Of a total of 179 verified individual records, 95 are from Falconiformes and 37 from Columbiformes, so that it cannot be doubted that these 2 orders contain true breeding hosts. The remaining 43 species are scattered among the Strigiformes (7 Strigidae), Galliformes (4 Cracidae and 3 Phasianidae), Psittaciformes (6 Psittacidae), Ciconiiformes (5 Ardeidae), Passeriformes (2 Corvidae and one each of Furnariidae, Cotingidae and Icteridae), Piciformes (3 Picidae and one Ramphastidae), Trogoniformes (2 Trogonidae), Caprimulgiformes (2 Caprimulgidae), Coraciiformes (one each of Alcedinidae and Momotidae), Cuculiformes (2 Cuculidae), Anseriformes (one Anatidae), and Gruiformes (one Eurypygidae). There is a possibility that the Psittaciformes, Galliformes or Strigiformes may eventually be found to furnish breeding hosts also.

Ornithoctona plicata. Probably the most common bird-fly of the Indo-Malayan, Australian and western Pacific areas, also found in the Madagascan Subregion, but not in continental Africa (J. Bequaert, 1941*b,* p. 266). Although the hosts are imperfectly known, they number at present 43 species of 10 orders. Two of the orders outnumber the others and unquestionably contain the chief breeding hosts: the Falconiformes, with 13 species in 7 genera of Accipitridae; and the Columbiformes, with 15 species in 9 genera of Columbidae (including the domestic pigeon). Four other orders possibly also contain birds suitable for breeding purposes: Galliformes (5 species: 2 Megapodiidae and 3 Phasianidae, including the domestic fowl and pheasant); Coraciiformes (2 species, one each of Alcedinidae and Bucerotidae); Strigiformes (2 species of Strigidae); and Psittaciformes (2 species of Psittacidae). In addition there are stray records from one species in each of the Orders Ciconiiformes (Ardeidae), Cuculiformes (Cuculidae), Trogoniformes (Trogonidae) and Passeriformes (Corvidae). The scarcity of records from passerines is remarkable; but very little attention has been paid thus far to the ectoparasites of these birds in the Indo-Australian area.

Stilbometopa podopostyla and *S. fulvifrons* are rather doubtfully distinct. Both are peculiar to the New World and mainly tropical flies. At present *S. podopostyla* is known from 10 wild species of birds, 9 of which belong to the two Orders Columbiformes (6 Columbidae) and Tinamiformes (3 Tinamidae), and are presumably effective breeding hosts. The remaining species of Passeriformes (Formicariidae) was almost certainly a stray host. In addition, there are a few records from the domestic pigeon, fowl and turkey. *S. fulvifrons* is reported mainly from Columbiformes (4 individual records on 3 species of Columbidae), no doubt true breeding hosts. There are a few scattered records from Cuculiformes (one species of Cuculidae) and Passeriformes (one species each of Icteridae, Cotingidae and Muscicapidae). Originally *S. fulvifrons* was described from Jamaica on the bob-white quail, *Colinus virginianus;* but this was a newly acquired host, introduced by Man from North America within recent historic times.

Ornithoica vicina (= *O. confluenta* of most American authors, not of Say). The most widely distributed American bird-fly, known from southern Canada to central Chile and common also in the Antilles. The large host list will no doubt be extended greatly by future collecting in the Neotropics. In the Nearctic Region, where the available data are fairly complete, the fly has been taken on 69 species of 7 orders; but only the Passeriformes and Strigiformes comprise true breeding hosts. Of 189 verified individual records, 144 are from 56 Passeriformes (69 on 19 species of Fringillidae, 35 on 21 Muscicapidae, 17 on 6 Corvidae, 14 on 5 Icteridae, 2 on 2 Paridae, 2 on 2 Thraupidae, 4 on an introduced Ploceidae, and one on Sittidae) and 31 are from 8 Strigiformes (Strigidae). The remaining verified records are scattered among the Ciconiiformes (2 on one Ardeidae), Falconiformes (one on Falconidae and 5 on 2 Accipitridae), Galliformes (5 on 4 Phasianidae, including one on the introduced domestic fowl), and Piciformes (one on Picidae). There is also one unverified record from Columbiformes (Columbidae). Among the passerines, the fly seems to favor certain genera and these are often preferred also by *Ornithomyia fringillina: Melospiza* has 24 records on 2 species (21 on *M. melodia*), *Zonotrichia* 7 on 3 species, *Turdus migratorius* 9, *Hylocichla* 6 on 4 species, *Spizella pusilla* 7, *Junco* 10 on 3 species, *Molothrus ater* 5, and *Pipilo* 11 on 3 species (5 on *P. erythrophthalmus*); but there is only one record each from *Dumetella carolinensis* and *Toxostoma rufum*. *O. vicina* differs decidedly from *Ornithomyia fringillina* in that it shows a marked preference also for Strigiformes. In fact, it is sometimes unusually abundant on owls, which may serve as permanent winter hosts in the northern parts of its range after the passerine migrants have left. In the Neotropical Region, the fly is known from 36 species of 8 orders and shows the same selectivity for Passeriformes (15 species: 3 of Muscicapidae, 3 of Tyrannidae, 3 of Corvidae, 2 of Furnariidae, 2 of Cotingidae, and one each of Thraupidae and Formicariidae) and Strigiformes (6 Strigidae). The remaining hosts belong to the Piciformes (5 Ramphastidae and one Picidae), Falconiformes (one Falconidae and 3 Accipitridae), Psittaciformes (2 Psittacidae), Tinamiformes (one Tinamidae), Columbiformes (one Columbidae), and Cuculiformes (one Cuculidae). There is a possibility that the toucans or Ramphastidae may be effective breeding hosts; but the matter calls for further investigation.

Ornithoica turdi. This is the African representative in the Old World of the American *O. vicina,* from which it is possibly not distinct; it occurs occasionally in the Mediterranean area. As recognized at present, it is known from 61 species of 9 orders, at least 4 of which contain effective breeding hosts: Passeriformes (27 species: 7 Muscicapidae, 7 Laniidae, 3 Oriolidae, 2 Sturnidae, and one each of Dicruridae, Prionopidae, Alaudidae, Pycnonotidae, Ploceidae, Corvidae, Campephagidae and Fringillidae), Falconiformes (10: 9 Accipitridae and one Falconidae); Cuculiformes (8: 5 Musophagidae and 3 Cuculidae); and Coraciiformes (8: 3 Bucerotidae, 3 Coraciidae, and one each of Alcedinidae and Meropidae). The Strigiformes (Strigidae) contain 5 host species and may possibly also serve for breeding purposes. The few occurrences on the following orders appear to be accidental: Piciformes (one species of Picidae), Columbiformes (one of Columbidae), and Galliformes (one of Phasianidae).

Ornithoica pusilla. A common fly in the Indo-Malayan area, Australia and the Pacific Islands, where it occurs probably on as great a variety of hosts as the two foregoing flies. At present it is known from some 46 species of 11 orders. The following 5 orders all seem to contain effective breeding hosts, although the available information is not fully adequate. The Passeriformes lead the list with 14 species (4 Pittidae, 2 Drepanidae, 2 Muscicapidae, 2 Sturnidae, and one each of Corvidae, Ptilonorhynchidae, Dicruridae, and Meliphagidae). The fly is recorded from 9 species of Alcedinidae, or kingfishers, in the Order Coraciiformes, these birds being greatly preferred hosts. It is also known from 5 Falconiformes (all Accipitridae), 6 Strigiformes (all Strigidae) and 5 Columbiformes (all Columbidae). There are single host species in the Gruiformes (Rallidae), Ciconiiformes (Ardeidae), Cuculiformes (Cuculidae), Caprimulgiformes (Podargidae), and Piciformes (Picidae), as well as records from 2 species of Psittaciformes (Psittacidae; in one case on an introduced parrot in Hawaii).

It is of some interest that the 18 species of Group D are all bird-flies. Moreover, they include nearly all the most frequently observed flies and most of those with the widest geographical distribution. Both features are clearly correlated with the greatly reduced host specificity, although it is not so evident whether the wide host range is the cause or the effect. It would seem that on the whole the more extended choice of hosts accounts for the more numerous captures, while the wider area covered by each species of fly may be due to the type of hosts selected rather than to the number of host species. Several of the favorite breeding hosts of the polyxenous hippoboscids are either marine birds addicted to very extensive roaming, or passerines and waders covering considerable territory during their periodic migrations.

A closer examination of the host relations of the polyxenous flies brings out another important fact. No species of hippoboscid can be said to be a general or indiscriminate parasite of either mammals or birds. Even the most promiscuous flies, such as *Ornithomyia avicularia, O. fringillina, Ornithoctona erythrocephala,* and *Ornithoica vicina,* use for breeding purposes birds belonging to only 2 to 5 of the 27 orders. Moreover, the large host lists of these flies are deceptive. Present knowledge of the host relations of even the most common flies is far too rudimentary to decide in each case which of their recorded avian hosts are actually effective for the survival of the species. For instance, in the case of *Ornithomyia fringillina,* of the 307 individual North American records I have verified to date from 95 native species of birds, 252, or 82 per cent, are from 75 native Passeriformes. Since North America harbors some 300 native species of passerines, it appears that only one-fourth at most are actively selected by this most common and least specific fly. Furthermore, the present list of 75 passerine hosts unquestionably contains several species to which *O. fringillina* strays only accidentally. Of the 252 individual records, 211, or 83.3 per cent, are from 59 species in the 3 families Muscicapidae, Fringillidae and Icteridae, the remaining 41 being scattered among 8 families. Even within the 3 favorite families a further selection by the fly is noticeable, and I predict that this will become more so in the future as more individual records accumulate.

General Conclusions. At present there is fairly conclusive evidence for the effective breeding hosts of 80 out of a total of some 124 recognizable described species of Hippoboscidae, namely 55 of some 90 bird-flies and 25 of 34 mammal-infesting species (exclusive of 5 flies of domestic animals). The knowledge of the host-parasite relations of these parasites is therefore sufficiently advanced to warrant drawing conclusions possibly of interest for the broader problem of animal parasitism.

1. Among parasites in general, the Hippoboscidae are rather unique in that they show an unusual diversity of types of host preference, with every gradation from species with extreme strict specificity to others using for effective breeding a variety of hosts in unrelated orders. This is the more remarkable as the family is a sharply defined, closely knit group, evidently with an ancient ancestry and probably now on the wane. It is in marked contrast with the type of host specificity of the other pupiparous ectoparasitic Diptera, the Streblidae and Nycteribiidae.

2. Of the 80 species discussed above, 24 are monoxenous, 24 oligoxenous, 14 pleioxenous, and 18 polyxenous. It is fairly certain that, when the host relations of these species are better known and positive information becomes available for the remaining 44 species, the proportions of these four groups will remain approximately the same. The relative numbers now in each group may be regarded as applying with minor changes to the family as a whole.

3. As was suggested in the concluding discussion of Group A, it is doubtful that the distinction between Groups A and B has any real significance from the point of view of host selectivity. It

should also be kept in mind that the limits of the vertebrate genera are subjective and sometimes even arbitrary. The monoxenous and oligoxenous species might be united to advantage. If all hippoboscids restricted to hosts belonging to one family are considered together as the more strictly specific parasites, it will be seen that they comprise slightly over half of the total (48 as compared with 44 in the combined Groups C and D). A sizeable number of Hippoboscidae are therefore as narrowly host-specific as is the rule in several other groups of ectoparasitic arthropods, a conclusion which may surprise some readers.

4. Host-specificity is decidedly more pronounced for the louse-flies of mammals than for those of birds. No mammalian flies are polyxenous and only 4 are pleioxenous, while 21 are either monoxenous or oligoxenous. On the other hand, the combined pleioxenous and polyxenous bird-flies (28) are about as numerous as the monoxenous and oligoxenous flies together (27). Among the bird-flies, those with a wide range of hosts covering two or more orders, are more numerous (18) than those of any of the other 3 groups. As these bird-flies are also the most widely spread and the most frequently observed, they are responsible for the prevailing belief that the Hippoboscidae in general exhibit little host preference.

5. All known species of Hippoboscidae are either strictly mammalian or strictly avian parasites. Occasional strays to the wrong Class of hosts do not detract from this statement since such strays are worthless for the survival of the species. Furthermore, except for *Hippobosca struthionis* of the ostrich, there is a sharp taxonomic demarcation between the mammal-inhabiting flies (subfamilies Hippoboscinae, Melophaginae, Alloboscinae and Ortholfersiinae) and those of birds (subfamilies Ornithoicinae and Ornithomyiinae).

6. On the subfamily level, host-specificity is less pronounced, except for the mammalian Melophaginae (on Artiodactyla only), Alloboscinae (on Primates only) and Ortholfersiinae (on Marsupialia only). The Hippoboscinae, however, have wild hosts in the Carnivora and Artiodactyla, and occur also on domesticated Perissodactyla. Among the bird-flies, *Hippobosca struthionis* is restricted to the Struthioniformes; but the Ornithoicinae and Ornithomyiinae comprise flies that breed on several orders, as shown in the summary of the known breeding hosts.

7. Within the several genera of bird-flies there is little evidence of uniformity or similarity in the host preferences even of closely related species. This is particularly striking in genera with a fair number of species, such as *Olfersia, Lynchia, Ornithomyia, Or-*

nithoctona, and *Ornithoica.* For instance, the American *Lynchia americana* and *L. fusca* are morphologically very similar, yet the former breeds successfully on Falconiformes, Galliformes and Strigiformes, while the latter is nearly restricted to Strigiformes. In *Ornithoica, O. confluenta* is highly specific of Ciconiiformes, while the closely related *O. vicina* breeds on a variety of Strigiformes and Passeriformes. Of the 12 genera of bird-flies which I now regard as distinct, 2 only, *Stenepteryx* and *Myiophthiria,* are strictly host-specific, the former occurring only on Hirundinidae and the latter only on Apodidae. As for *Crataerina,* while the several Old World species are restricted to Apodidae, the one American species lives on Hirundinidae, which belong to a different order.

In the case of louse-flies described from unknown hosts, it is safe enough to decide from their generic characters whether they came from mammals or birds. It is impossible to go beyond this, however, and to make even a plausible guess as to which order the hosts belonged.

8. Hippoboscid specificity is in general of the *ecological* type. Every species of fly tends to adopt as regular breeding hosts mammals or birds with similar habits and habitats, regardless of their taxonomic or phylogenetic affinities, or hosts which have some regular ecological connection (such as the predatism which brings together the birds of prey and the passerines). Of course, ecological similarity of the hosts frequently occurs within the limits of the higher taxonomic units, such as orders and families. Other aspects of this problem will be discussed in Part II in connection with the evolution of the flies.

Strict specificity is sometimes purely fortuitous, as I pointed out before for some of the monoxenous species. In other cases, it may be merely the result of geographical isolation. For instance, the Ortholfersiinae of Australia are now restricted to the Marsupialia, perhaps merely because the other autochthonous mammals of that isolated region are of types unsuited to the Hippoboscidae and avoided by these parasites also in other parts of the World.

In recent years, students of certain groups of parasites, especially of lice (Anoplura and Mallophaga), have concluded, from the present distribution and host relations, that the phylogenetic relationship of the parasites, as expressed by their taxonomy, frequently reflects that of the hosts. These conclusions have been embodied in the following "rules" (Eichler, 1948*b*). (*a*) Fahrenholz's rule that the natural or phylogenetic classification of some groups of obligate and permanent parasites corresponds with that of their hosts, so that the ancestors of extant parasites must have been parasites of the ancestors of extant hosts and the evolution of both hosts and parasites was simultaneous. (*b*) Szidat's rule that, in addition, there are parallelisms between the hosts and their permanent parasites in the evolutionary specializations of their structures, primitive hosts being parasitized by primitive parasites and specialized hosts by specialized parasites. (c) Eichler's or the divergence rule that isolated groups of hosts often do not harbor very many kinds of permanent parasites, while comparable groups of hosts with many species or near affinities to other groups of hosts may carry, not only many species of parasites, but also parasites differentiated into many genera which may live together on the same host species.

These rules seem to apply best to groups of parasites that spend the whole of their existence in or on the same host; but they do not work well for even wingless parasites, such as fleas and ticks, in which some of the stages are free-living or develop on different individuals or species of hosts. Our survey of the host-parasite relations of the Hippoboscidae discloses no clear-cut case where any of the three rules might lead to interesting conclusions. It is not possible to use the host preferences of these flies as corroborative evidence in cases where the taxonomic position or phylogenetic relationships of the host are uncertain or disputed. The louse-flies have clearly selected their hosts regardless of the hosts' phylogenetic affinities and, so far as the genera and species are concerned, the hippoboscid evolution has followed its own independent course. Host choice has been determined by structural specialization and environmental factors, the latter involving such diverse matters as availability, macroclimate, microclimate, and peculiarities of the structure, physiology and behavior of the hosts. It is dominated by the requirements for successful reproduction of the flies, these requirements deciding the breeding hosts of each species. The great majority of the Hippoboscidae, being fully endowed with the power of flight, are extremely mobile and not narrowly restricted in their choice among the several available potential hosts.

9. The degree of specificity tends to be correlated with the degree of specialization of the fly, the more generalized species usually occurring on many unrelated hosts and the most specialized always being strictly host-specific (*Melophagus, Allobosca, Crataerina, Stenepteryx,* and *Myiophthiria*). This matter also will be con-

sidered in the discussion of the evolution of the Hippoboscidae in Part II.

Hippoboscidae Biting Man. No known hippoboscid numbers Man among its normal or habitual hosts, although several species may be induced by starvation to bite and even to feed if placed on the human skin, and a few will also attempt to bite people spontaneously in the open. Experiments with *Hippobosca equina, Melophagus ovinus,* and *Lipoptena cervi* fed on Man were described in the section dealing with the mechanism of feeding; but in no case did a louse-fly produce a viable larva on human blood alone. Coatney (1931), in Iowa, found that *Pseudolynchia canariensis* bit Man readily in captivity, sucking blood for 1½ to 10 minutes, pain being seldom felt at the time. A red, itchy, round wheal appeared the next day at the site of the bite, persisting for 6 days in one person, for 9 days in another and for 20 days in a third. The itching was particularly severe in the evening and early morning. A male was kept alive for 12 days on human blood; but females lived for only 7 days at most on this diet, during which time they never produced a larva. Galli-Valerio (1912, p. 305), in Switzerland, induced an *Ornithomyia avicularia* to bite himself, after the fly had been removed from a short-eared owl, *Asio f. flammeus* (= "*Otus brachyotus*").

Observations of Hippoboscidae biting people spontaneously are more interesting than laboratory experiments, as they raise the possibility of the flies becoming involved in the accidental or mechanical transmission to humans of pathogenic infections of animals. Great care should therefore be taken to accept only fully substantiated reports of such occurrences. Even educated but uninformed or uncritical persons are prone to believe that they are being bitten by insects, when they are merely annoyed by their settling or crawling on the skin or in the scalp or beard. In some cases they may even imagine feeling the prick of the bite. Entomophobia is a widespread ailment of the human race, and in some persons it verges on hysteria.

Hase (1940) published a summary of the hippoboscids reported to attack people and his work should be consulted for further details. The present review is restricted to the essential facts and adds a few cases not mentioned by Hase. I have tried to include only cases of flies that were definitely biting and not merely annoying by their presence or in some other way.

1. *Hippobosca equina* Linnaeus. Réaumur's (1742) account of how this species feeds was based on a fly that bit him spontane-

ously indoors, after escaping from the container in which it was confined.[27] Hase (1927, p. 212) states that *H. equina* often flew onto him and bit him in Spain and the Balkans. He describes the effects of the bite (1927, pp. 234–235) as noted in experiments and also figures (1940, p. 642, fig. 1) a female that engorged fully on his arm, where it had alighted of its own accord, when at liberty. He says that this fly will bite even through thin clothing and that the prick and the boring in of the haustellum were not or barely felt. At the time of the bite there was a slight reddening at the spot and a little blood oozed from it after the fly left. No further after-effects, such as itching, swelling or formation of a pimple or a pustule were noticed. Aschner (1931, p. 370), in Palestine, saw *H. equina* liberated in the laboratory fly onto people and attempt to bite, confirming Réaumur's earlier observation. Hesse (1931), in Germany, reports that in August, 1930, *H. equina* bit him spontaneously on the hand in his house in Berlin. The bite felt about like that of *Haematopota* and left no redness, swelling or any other after-effect. Séguy (1936, p. 110) also describes the effects of the bite on a person in experiments. M. Leclercq (1949) states that, in Italy, one of the flies he had collected alive from a horse, after escaping in his room the same evening, bit him on the face and another person in an adjoining room a few hours later. Pic (1915), in France, mentions a *H. equina* remaining on a person for 24 hours, but does not state that it did bite.

2. *Hippobosca camelina* Rondani is only rarely mentioned as biting people, possibly because this is a common occurrence. Brumpt states (1936, **2**, p. 1363) that he was often bitten by it in Africa while performing autopsies of camels, and describes the bite as not painful, though leaving a slightly itching pimple. Mr. H. Hoogstraal sent me a specimen caught in the act of biting a person in the Nubian Desert, 60 miles south of Assuan, Egypt. I recorded (1939*b*, p. 89) that J. G. Myers was bitten by *H. camelina* in the Red Sea Hills, Sudan.

3. *Hippobosca variegata* Megerle (= *H. maculata* Leach). Hase at first (1927) included this among the species biting man, but he omitted it later (1940). Austen (1909, p. 174) presented evidence of its biting people in Ashanti and India; but he added that, according to F. Smith, some natives in India deny that it ever bites, while others claim that it does at times. In Ashanti, R. Cope

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[27] Paullini's (1688) account of louse-flies annoying Man in the open, in Westfalen, Germany, concerns *Lipoptena cervi*, not *Hippobosca equina* as might be surmised. Actual biting was not mentioned.

stated that a female bit him on the forearm near the elbow, on the porch of a house. A. M. Elliott, in India, induced it to bite by placing it on his arm. According to Schuurmans Stekhoven (1923*a*, p. 73), in Indonesia it attacks people rarely. He observed while crossing rivers that, if the water reached up the belly of his horse, some flies settled on his clothes, neck, face and hands and one of them occasionally bit. He adds that ''the bite is at first somewhat painful; but this sensation disappears rapidly and I have never noticed any itching or formation of blisters.'' Mr. H. Hoogstraal observed a male biting a person at Tsiomb, Madagascar, November 8, 1948.

4. *Hippobosca longipennis* Fabricius (= *H. capensis* v. Olfers). Although this louse-fly is abundant on domestic dogs in the Near and Far East, it has been seldom mentioned as biting people. Perhaps this happens so often that it is no longer noticed by the native population. The following two records are the only ones I have been able to trace. Wenyon (1911, pp. 292 and 299) states that, in the course of his work on Oriental sore at Bagdad, he was only bitten on two occasions, though he lived in close association with several infested dogs. Gachet (1915) mentions, also in connection with work on Oriental sore, that two persons were bitten in Iran.

Hase (1927) originally listed the South African *Hippobosca rufipes* v. Olfers among the louse-flies attacking Man; but he did not mention it again later (1940). Distant (1892, p. 244) reports that, in the Transvaal, it often attached to his neck, although he does not claim that it ever bit him.

5. *Melophagus ovinus* (Linnaeus). The sheep-ked is the louse-fly most often observed biting Man, due, no doubt, to its abundance on sheep in many places and to the ease with which it can pass to people, particularly at shearing time. Shepherds, sheep-shearers and workmen handling fresh wool or fleece are most commonly bitten. Zetterstedt (1848) stated a century ago that sheep-ked bite produces a swelling similar to that made by tick bite. The effects of the bite of *M. ovinus* on Man were described by Freund and Stolz (1928) and by Kemper (1951, p. 244). In most cases they are very mild, even the pricked spot being sometimes difficult to discover afterward; in some persons, however, the bite produces itchy papules 6 to 10 days later. People who are bitten repeatedly probably become more or less immune, their skin no longer reacting to the bite. Although keds have often been made to bite Man in experiments, they could not be kept alive on human blood for more

than two weeks, during which time they never voided a viable larva. (For further references, see J. Bequaert, 1942*a,* p. 188).

6. *Lipoptena cervi* (Linnaeus). The deer-ked is often claimed to bite Man in Europe, but there are actually few precise observations confirming such statements. In this case particularly, laymen and hunters are apt to believe that they are bitten, when they are merely annoyed by the crawling motions of young, volant flies over the skin or in the hair. Accounts, such as that by Schroeder (1911), in Germany, which speak only of the flies "attacking" are here disregarded, the term being too vague. That *L. cervi* does not bite Man as freely as is generally believed and stated in text-books, is further substantiated by Hesse's (1931) remark that, although countless deer-keds flew onto him in the course of many years in Germany, not a single one ever bit him. An interesting observation on *L. cervi* by Villeneuve (1913), in France, is here quoted in full; because it suggests how in some cases deer-keds may be believed to bite, when the pain they cause is actually not due to the action of the proboscis: "While crossing a stand of high timber in Rambouillet Park in November, toward 1 P. M., I felt suddenly a burning pain in the scalp, first in the parietal region and later another near the back of the neck. I removed with great difficulty, in a battered and mutilated condition, two young winged specimens of this species. I can assure that this insect has terrible claws."

Hase (1939) described the reactions of the human skin to the bite of *L. cervi,* as observed on himself in laboratory experiments. The prick itself and the boring in of the haustellum were scarcely felt, if at all, the spot showing only a slight reddening, and no lump or swelling; but secondary skin reactions set in two or three days later, persisting for some time and culminating about the 14th day. They were perceived even after 20 days and marked by severe itching, occurring spontaneously during the day as well as at night, but without rise of temperature at the itchy spots. A red halo surrounded the puncture within 24 to 48 hours after the bite, when a fairly indurated pustule with a small central blister also appeared. As a rule the blister eventually broke open, oozing a droplet of blood and serum, which later dried at the center of the pustule; the process being repeated several times. Some of the pustules reached 3 or 4 mm. in diameter, others only 0.5 to 1 mm. Brumpt (1936, **2**, p. 1364) also had observed previously that the experimental bite of *L. cervi* in Man is at first hardly noticed, so that the bitten spot cannot be traced after the fly leaves; but that the next day a hard, urticating papule appears and persists for 15 days.

The following appear to be *bona fide* reports of *L. cervi* biting Man spontaneously in nature. Scholtz (1848) first mentioned a case in Germany. Since Hase (1939, p. 417) states explicitly that his collector Gosswald developed itchy pimples 24 hours after the bites, the keds must have bitten while they were caught in the open in Germany. Eichler (1939, p. 211) himself was only annoyed by the volants flying onto him near Berlin; one E. Sperling assured him that keds sometimes bit people. Kruseman (1937) states that, in East Prussia, while tracking elk in early October, many *L. cervi* flew onto him and his companions. They usually alighted on the neck and behind the ears and started biting immediately. He describes the bite as painful, but the pain disappeared rapidly and no swelling was produced, which makes it rather doubtful that the flies were actually biting in this case.[28]

7. *Crataerina pallida* (Latreille). Most of the observations of people being bitten spontaneously by hippoboscids relate to this common specific parasite of the European chimney swift, *Apus apus*. Swifts often choose fairly permanent nesting sites in sheltered places of buildings, particularly in cities, and may return to the same site year after year. Swifts and swallows have acquired in Europe the status of welcome guests, being protected by custom or law, so that they and their parasites thrive without hinderance or check. As explained before, *C. pallida* larviposits in the hosts' nests, where viable puparia accumulate in late fall and survive through the winter. Upon emerging the following spring before the normal hosts return to the nests, or when they become unusually abundant later in the season, the hungry flies, wandering about in search of food, frequently enter rooms adjoining the nesting sites and may then bite people either at night in bed or during the daytime in the open. Thus they become sometimes a real, though temporary household pest.

The two European flies of swifts (*C. pallida*) and house martins (*Stenepteryx hirundinis*) are so often confused, even by entomologists, that it is occasionally doubtful to which species published accounts of their biting people actually refer. A case in point is the often quoted observation by P. J. Van Beneden of swift flies attacking patients in a hospital at Louvain. The earliest account of the case by Gervais and Van Beneden (1859, **1**, p. 391) called the fly "*Ornithomyia pallida*" (= *Crataerina pallida*), which I assume to be the correct name, since the flies were said to live normally on swifts. In a later account, however, Van Beneden (1875, p. 114) changed the name to "*Ornithomyia hirundinis*" (= *Stenepteryx hirundinis*). He now added that the flies had entered the hospital ward through open windows at night and that in the morning the bodies of several patients and the sheets of their beds were blood-stained following the bites.

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[28] Some of the published statements of *L. cervi* biting Man are of a general nature and repeated again and again, although not based on personal observations. R. Blanchard's (1890, **2**, p. 294) claim that P. J. Van Beneden observed winged *L. cervi* on Man in a hospital at Louvain, Belgium, shows a complete misunderstanding of the case (see under *C. pallida*). Brumpt (1949, **2**, p. 1347; also in earlier editions) refers Van Beneden's observation by error to *Ornithomyia avicularia*.

The following more recent reports of *C. pallida* biting Man are arranged by countries.

a. Norway. Natvig (1941) reports an interesting case in Oslo, where the flies were a persistent blood-sucking pest in the upper rooms of a house during two successive summers, so much so that they had to be dealt with by professional exterminators.

b. Germany. Hesse (1919, p. 408; 1920, p. 33; 1929, p. 70) reports several house infestations by this fly at Leipzig and near Berlin. In one case a fly fully engorged with blood was found in a bed. Specimens were running over curtains and rugs and one fly that dropped from a curtain on a person's neck, bit at once. Christeller (1924, p. 103) himself was bitten on the neck while standing near an open window in a room near Berlin; the bite, he says, was much like that of a mosquito. Eichler (1939, pp. 215–216) describes a heavy infestation of a commercial office in the center of Berlin during two successive summers (1935 and 1936), the flies actually biting people. In his two other cases, at Berlin and Hannover in 1939, the flies are only said to have been annoying by their presence, biting not being mentioned. Hase (1940, pp. 648–649) reports two further cases at Berlin, where the flies were annoying in houses in 1938 and 1939, but possibly did not bite. Kemper (1951, p. 226) gives a detailed account of heavy infestations in several buildings, also in Berlin, but how often the flies did bite people is uncertain. Madel (1949) mentions flies attacking people in a house at Freiburg. Kemper (1951) had at first some difficulty in making *C. pallida* bite himself or other persons in captivity. He was more successful later in the season, using flies that had been first kept alive for some days on swifts. He is inclined to believe that only the older flies will readily bite Man. Of four flies fed only human blood from August 5 on, 3 lived until August 11 and one until August 16. The pain produced by the prick of the proboscis was very slight, as a rule, and a reddish spot persisted at the bite for about 3 hours. No further after-effects were noticed. Weidner (1952, *Mitt. Hamburg. Zool. Mus. Inst.*, **51**, p. 123) reports an additional case of *C. pallida* biting people in Hamburg.

c. France. Guiart and Lesieur (1913) report a case at Lyons of a woman being bitten repeatedly in an attic room, on the face and neck during the day and over the whole body at night. The bites were not particularly painful, but were followed by pimples, itching, redness, and eventually scabs. The flies were particularly inclined to infest the bed. Numbers of them would come in by the window, as many as 15 being killed on one occasion.[29] Moutier (1928) found, presumably in France (the locality not being given), two specimens of *C. pallida* on the back of the neck of a woman, the area involved also showing scratch lesions; he does not state definitely, however, that the flies had been biting.

d. Belgium. In addition to Van Beneden's case mentioned before, M. Leclercq (1948) reports another, at Liege in July, 1948, the flies presumably having been brought from the country in the person's clothing. According to Bernard (1952), in July, 1951, many swift flies invaded army barracks at Liege, annoying the soldiers.

e. Switzerland. Galli-Valerio (1922, p. 344; 1932, p. 141; 1933, p. 424; 1935, p. 326; 1939, p. 1155) reported several cases of *C. pallida* biting people at Lausanne. Some flies, captured while biting persons indoors, refused to bite him later in captivity. He studied the effect of the bite and observed in an infested house one of the flies that had settled more or less permanently on a cage-bird (*Munia* sp.).

8. *Stenepteryx hirundinis* (Linnaeus). According to Séguy (1936, p. 115; 1939, p. DCCXXIV), this species does not live well in captivity and is reluctant to bite Man. He states that "the bite is more painful than that of *Hippobosca:* I have had experience with it. It does not leave an indurated red circle and the insect takes much more time to engorge with the host's blood. It

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[29] Although the authors refer their observation specifically to *C. pallida,* Brumpt (1949, **2**, p. 1347) cites it under *Stenepteryx hirundinis,* which he, moreover, gives erroneously as the usual parasite of swifts.

may bite cage-birds experimentally in lieu of swallows.'' The earliest account of *S. hirundinis* biting Man spontaneously is by Kirby and Spence (1815, **1**, 1st Edition, p. 122, footnote; 1816, **1**, 2nd Edition, p. 112) in England: ''The swallow-fly (*Ornithomyia hirundinis,* Latr. *Hippobosca* L.), whose natural food is the bird after which it is named, has been known to make its repast on the human species. One found its way into a bed of the Rev. R. Sheppard, where it first, for several nights, sorely annoyed a friend of his, and afterwards himself, without their suspecting the culprit. After a close search, however, it was discovered in the form of this fly, which forsaking the nest of the swallow, had by some chance taken its station between the sheets, and thus glutted itself with the blood of Man.'' As Kirby and Spence seem to have separated *S. hirundinis* from *Crataerina pallida,* their observation probably referred to the true *Stenepteryx.* Eichler (1937, p. 269; 1939, p. 216) states definitely that he was bitten spontaneously on the back of the hand by this species, while examining nests of house martins, *Delichon urbica,* near Göttingen, Germany. The painful bite felt like a bee sting, but produced only a slight swelling which disappeared soon afterward. This was the only attack he ever experienced, although some flies remained in his clothing for 1 or 2 days after he handled house martins.[30] He records another interesting case of *S. hirundinis* settling on a canary bird in a cage, after the fly had been brought accidentally in the room. Schöyen (1916) mentions *S. hirundinis* attacking Man at Oslo, Norway; but he may have confused *C. pallida.* Johnsen (1948), however, records a true *S. hirundinis,* sent to him as having bitten people in a house in Copenhagen, Denmark; the bites were said to be very painful and to cause swellings about one centimeter in diameter.

9. *Ornithomyia biloba* Dufour. This species is the specific parasite of the European barn swallow, *Hirundo rustica.* I refer to it the seven cases of supposed *O. avicularia* reported by Galli-Valerio (1907, p. 532; 1910, p. 44; 1921, p. 350) as having bitten people in rooms in Switzerland, since the author states that the flies came from swallows' nests.

10. *Ornithomyia avicularia* (Linnaeus). Eichler (1939, p. 214), possibly misled by erroneous published statements, implies that this common bird-fly frequently attacks Man. In the fore-

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[30] Guiart's observation, which Eichler quotes after Falcoz, referred to *Crataerina pallida,* where I have cited it. Séguy (1939) also cites it by error for *S. hirundinis.*

going paragraph, I referred to *O. biloba* several of Galli-Valerio's cases of so-called *O. avicularia* biting people in Switzerland. Only the following reports seem to be fairly reliable for the species, although possible confusion with *O. fringillina* cannot be ruled out. Kirby and Spence (1816, **1**, 2nd Edition, p. 113) relate the following: "In travelling between Edam and Purmerend in North Holland (July 21, 1815), in an open vehicle, I was much teased by another bird-fly (*Ornithomyia avicularia,* Latr.) (two individuals of which I caught) alighting upon my head and inserting its rostrum into my flesh." Galli-Valerio (1910, p. 44; 1912, p. 305) reports two cases from Switzerland: in one, a fly leaving a tree pipit, *Anthus trivialis,* flew onto a person and bit at once; in the other, several flies from a European short-eared owl, *Asio f. flammeus,* bit him three times in the armpit, causing oedema, redness and itching. Vogel (1935, p. 53) relates that in Oberhessen, Germany, *O. avicularia* often flew onto people, but did not attempt to bite. M. Leclercq (1946) records one of these flies that bit a person's neck in July, 1943, at Bellaire, near Liege, Belgium.

11. *Stilbometopa podopostyla* Speiser. This strictly American bird-fly is a frequent parasite of wild pigeons (Columbidae), occasionally also of domestic pigeons and certain other birds. Howell and Stiles (1941) published the remarkable case of a fly, which I identified as this species, biting a person indoors on the neck in the region of the submaxillary gland, at about 7:15 A. M., at Ponca City, Oklahoma. The bite itself was not painful and was described by the person as resembling "strong suction more than an insect bite." The after-effects were, however, most unusual. At about 9:45 A. M. "the patient suddenly found her vision blurred and lost the use of her arms and legs; vertigo was extreme and her head ached severely. There was a slight local swelling and inflammatory reaction at the site of the insect bite, and considerable tenderness of the gland was manifest. She was admitted to the hospital at 10 o'clock, showing symptoms of acute toxemia, slightly subnormal temperature (about 97.5° F.) and severe headache. The patient showed a pulse rate of 100, vertigo, weakness, fleeting pains in the joints, abdominal soreness, increased respiration, tremors and chilly sensations. She exhibited nervousness, but did not vomit, nor was she nauseated; nausea and vomiting are commonly present in such conditions. The appetite was poor and her food was not relished. Medication consisted of opiates to control the nervousness and supportive treatment. Symptoms persisted after 28 hours; how-

ever, the patient apparently had returned to her normal condition within a few days.'' This case, the first of its kind for the Hippoboscidae, can best be explained on the assumption that the patient was hypersensitive or allergic to some protein injected by the bite, presumably with the fly's saliva.

12. *Pseudolynchia canariensis* (Macquart) (= *Lynchia maura* Bigot). Considering the prevalence of pigeon-flies and the proximity of pigeon coops and lofts to human quarters, it is rather surprising that this species has been so rarely observed biting humans of its own accord. It may be induced to bite Man experimentally as shown by Coatney's (1931) observations cited above. Drake and Jones (1930), in Iowa, remark that, while collecting several hundred flies for their studies, many settled on the exposed skin and on clothing, but that none ever did bite them. On the other hand, Bishopp (1929), in the United States, claims that the flies bite Man frequently, especially where squabs are prepared for market, the laborers often complaining of bites: ''There is a considerable difference in the susceptibility of individuals to the attack of the fly. In some cases bites have resulted in marked swelling, stiffness of joints, and soreness in the parts attacked, symptoms which may persist from one to three days.'' Levi (1941, p. 320) says that on himself the bite of the pigeon-fly continued slightly painful for 5 days. In February, 1948, Dr. N. A. Weber took a male of *P. canariensis* biting a person indoors at Mutwanga, Belgian Congo, on the West side of Mt. Ruwenzori.

13. *Olfersia coriacea* van der Wulp. This is a fairly common Central and South American parasite of certain gallinaceous game birds. When the hosts are killed the fly alights occasionally on the hunters, as all bird-flies may do. In Yucatan and the adjoining section of Guatemala, it is believed that it bites people freely and, furthermore, that it infects Man with cutaneous leishmaniasis (''bay sore'' or ''*ulcera de los chicleros*''). I have been unable to obtain so far definite and fully reliable proof that *O. coriacea* actually bites humans; although it should be mentioned that Lutz, Neiva and da Costa Lima (1915) reported their *Pseudolfersia meleagridis* (a synonym of *O. coriacea*) as biting Man in Brazil, before the species was accused of transmitting a disease in Central America.

Apart from the unusual case of *Stilbometopa podopostyla* and the few more definite reports for *Pseudolynchia canariensis*, there are no records of any bird-flies biting people in North America. Furthermore, although volant adults of *Neolipoptena ferrisi* and

Lipoptena depressa, of American deer, often occur in swarms and alight on people, apparently there are no definite statements of their biting Man in nature. Hare (1945), in his detailed study of the behavior of newly-emerged, winged *L. depressa,* in California, observed several hundred specimens on himself and on others, yet mentions no instance of a fly biting, an occurrence which he would not have failed to note. Several reliable observers, who had much experience with these flies in the field, have assured me that they were never bitten by them.

Effect of the Parasite on the Host. True parasitism is strictly a one-sided relation, in which the benefits of the association between the two organisms, host and parasite, accrue only to the parasite. In the case of blood-sucking permanent ectoparasites, such as the Hippoboscidae, there is not a shred of evidence that they give anything in return to the individual host for the food and shelter they extort. At best, the parasite helps prevent overpopulation of the host species or may have a more general rôle in natural selection by weeding out the least fit of competing individuals or species. In either view, however, the parasite remains detrimental to the individual host. Nor can I see the need to gloss over the supposedly sinister implications of the word ''parasitism'' by twisting it into a mere, presumably aberrant form of symbiosis. Of course, I am quite ready to grant that all associations of organisms, even the most altruistic, are tainted to some degree with parasitism.

It is more important to realize that it is in the parasite's own interest to limit the damage it inflicts on the host. It is essential for the survival of the parasitic species that it must never endanger the survival of the host species nor reduce the host's population to the extent that future generations of the parasite have no longer a reasonable chance of reaching the proper host. This becomes increasingly important when progressive specialization of the parasites restricts their suitable hosts to a few or even to one species. The Hippoboscidae seem to have solved this delicate problem of adjustment to the point of perfection. Their very low rate of reproduction, determined by the peculiar adenotrophic viviparity, results in a generally low density and frequency of population, as shown in a previous section. In the case of many bird-flies in particular, the infestations may be so light that the damage done to the birds is probably negligible and that the host-parasite relation almost dwindles to tolerance by the hosts. It may be noted once more that the frequently heavy louse-fly infestations of domestic animals are abnormal and due to the debilitating influence on the host of close association with Man.

The immediate or direct effects of the "bite" or feeding process on the normal host are as a rule narrowly localized and transitory. The sensation of pain or discomfort and the mechanical injury following the puncturing of the skin and the probing of the subcutaneous tissues, vary even for the same species of fly on different individuals of one host, so far as can be judged from observations made on abnormal hosts, such as domestic animals and Man. The variations may be due to many causes, such as the number of probings by the proboscis, the site of the bite, the depth reached in the tissues, and the distance of the bite from nerve endings. Some of them are also subjective, certain individuals being more sensitive or paying more attention to the bite, which explains the contradictory statements regarding the effects of the bites on humans. The scratching, crawling or running movements of the fly sometimes seem to be more annoying than the bite itself and, in humans, may even be mistaken for it. In animals they often cause more violent defensive reactions. The unusually sharp claws scratch the skin and pull on the hairs or feathers wedged in the deep cleft between the heel and the tooth or between the double teeth. Evans (1895, p. 79) quotes an informant from India ("J. B. D.") for the dog-fly, *Hippobosca longipennis* (= *canina*), as follows: "So sharp is the claw that the hair grasped by it is cut into shavings like wood by a carpenter's plane." This statement would seem to call for corroboration.

The mechanical injury of the skin and subcutaneous tissues may cause at first a slight bruise or redness followed by inflammatory reactions. The later and more persistent effects of the bite may be itching and local swelling into a papule or wheal. Lester and Lloyd (1928) showed that the skin reactions to the bite of tsetse-flies are due mainly to the injection of foreign proteins contained in the salivary secretion of the flies. If a *Glossina tachinoides* bites after removal of the salivary glands, it causes no wheal even in a very susceptible person. Wheals can also be produced experimentally in sheep by injecting the skin with an emulsion of tsetse-fly salivary glands in saline. Although the saliva which passes into the host must be regarded as a loss to the fly, it has been shown that a considerable quantity may so escape, particularly when a tsetse-fly bites but fails to feed. There are no comparable experiments for any of the hippoboscids, but it seems reasonable to assume that their saliva produces similar reactions. It has been claimed that the normal, uninfected saliva of a blood-sucking insect is harmless to the skin and tissues of an individual host bitten for the first time, reactions occurring only after the host has been sensitized by previous bites of the same species (Gordon, 1950). This theory is scarcely supported by the observations of hippoboscids biting humans, discussed in some detail in the preceding section. Some free-living hematophagous Diptera, which must engorge as quickly as possible, commonly use so-called ''pool-feeding'' in obtaining a meal. The laceration of the tissues by the proboscis causes extravasated blood to form a hemorrhage beneath the epidermis, large enough for the fly to fill rapidly with blood. The hemorrhage may continue to spread after the bite ceases and even invade the muscle layers, producing at the locus of the bite a small red subepidermal spot which later turns black. This method of feeding is usual for the black-flies (Simuliidae). According to Gordon and Crewe (1948, *Ann. Trop. Med. Paras.*, **42**, pp. 334–356), it is often used by *Glossina*. There is no evidence of this for the Hippoboscidae, no distinct hemorrhagic spot having ever been reported following their bite.

H. and J. R. Michener (1936, p. 105) report the following unusual occurrence from southern California: ''In one instance it seemed that flat-flies (Hippoboscidae) were responsible for the loss of the head feathers of a young, hand-reared mockingbird [*Mimus polyglottos*]. Its favorite perch was in a window in front of which all the birds were banded and the flat-flies leaving the birds alighted on the window panes. It was noticed that the feathers of the mockingbird's head were getting thin and rough in appearance, and upon closer examination the fore part of the top of the head was found to be matted with flat-flies, about ten being removed. All the feathers fell off this part of its head and were not replaced until the molt.'' Unfortunately the species of fly was not ascertained. A curious feature of this case, not mentioned by the authors, is that, in spite of the obvious ill-effects of the flies, the bird did not attempt to get rid of them in response to the irritation they must have caused.

No doubt the general health of the host is affected to some extent by the loss of blood at the frequent feedings; but it is difficult to appreciate the resulting injury objectively. I summarized in a previous section the available information on the size and frequency of the blood meals and concluded that the data were inadequate to calculate the total amount of blood consumed by one fly during its average life. Nevertheless, in the case of heavy individual infestations, the daily loss of blood should be of consequence. Perhaps it is most serious for nestling birds, on which the flies often tend to congregate, in which case it may be responsible at times for an increased juvenile mortality.

Most veterinarians and sheep breeders are emphatic that *Melophagus ovinus* does considerable damage to sheep by the irritation of the bites, the constant drain on the blood, the staining of the wool, or in other ways (J. Bequaert, 1942*a,* pp. 197–198). Actually, experimental data bearing on the subject are few and unsatisfactory. Mote (1922), in Ohio, compared the growth of 5 lambs heavily infested with keds and lice with that of 2 lambs free of keds and with only a few lice. He concluded that the heavily infested lambs were the only ones not to gain weight; but the differences shown in his tables between the two groups are not too striking. Imes (1917) quotes estimates by sheep owners, in Utah, of annual average losses of 20 to 25 cents per head due to keds in heavily infested flocks. It is a question whether the actual losses incurred justify the expenditure of time and material needed for effective control.

Kemper (1951, p. 237), in Germany, found 37 engorged *Crataerina pallida* in a nest where a pair of swifts had been brooding and estimated that twice that many had been feeding on the birds. He calculated that if both parents shared the brooding equally and 50 flies fed on them, each fly imbibing 25 mg. of blood every 5 days, each swift would daily lose 0.125 g. of blood during the brooding season, a sizeable amount considering that a European swift, *Apus apus,* weighs only 33.4 gm. on the average. These calculations are impressive, but the author seems to have overlooked that most of the flies present in the nest must have fed on the nestlings and not on the parents. Nevertheless, a heavy infestation could conceivably incapacitate a swift, and there are some records of swifts found dead or dying and heavily infested with flies, as noted in the section on the population dynamics. Usually, however, it is difficult to decide whether death was due to the infestations or to other causes. Some ornithologists seem to be unduly disturbed by the ''ugliness'' of the bird-flies, which may lead them to rather far-fetched conclusions. One ingenious naturalist, noticing a fly on a dying swift which had suffered a neck injury presumably by striking a wire, suggested that the injury ''probably was caused through the parasite taking a vicious 'bite' at an awkward moment.''

The host's health may also be impaired indirectly by hippoboscids acting as vectors of certain pathogenic micro-organisms, especially Protozoa. Such transmissions might be more serious for the birds than the injury and discomfort inflicted directly by the bite and feeding. Many birds and mammals are known to harbor micro-organisms, chiefly in the blood, some of them harmless and others causing disease. Blood-sucking arthropods unavoidably take up such organisms, and if these are able to survive or to multiply in the arthropod, the possibility arises that it may inoculate them successfully to an uninfected host either at a future feeding or by other means. The section on the parasites reviewed the various bacteria, Protozoa and related organisms reported from the Hippoboscidae. Some of these will now be discussed more fully from the point of view of their rôle in disease.

Hippoboscidae have often been suspected or blamed for the transmission of endoparasites of vertebrates, but most of these claims lack experimental proof. Some of them are based on mere surmises or even on misunderstanding. The extent to which hippoboscids maintain or spread disease is sometimes of practical importance, for instance to sheepmen and pigeon breeders. It has also far-reaching theoretical implications, as it might be in some cases a decisive factor in regulating the population dynamics of the flies' hosts. Observations and experiments bearing on the subject should therefore be carried out with the utmost care and the results should be subjected to rigorous criticism. No conclusions should be drawn or accepted that are not fully substantiated by facts. It seems appropriate to dispose of the several spurious claims of hippoboscid transmission, some of which have found their way into textbooks and will now be hard to root out. Unsuccessful attempts to transmit certain diseases will also be noticed.

I discussed before the claims that *Melophagus ovinus* and *Hippobosca rufipes* might at times spread anthrax (*Bacillus anthracis*) mechanically by means of the infected mouth-parts. The statement by Eysell (1924, p. 382), repeated by Maass (1937, p. 162), that the ''Hirschfliege (*Lipoptena cervi* L. ?),'' in Utah, transmits tularemia (*Pasteurella tularense*) was based on a misunderstanding of the vernacular ''deer-fly,'' which in North America refers to certain tabanids (*Chrysops*), not to the deer-keds. Tabusso (1917, p. 470) describes an unsuccessful attempt to transmit enzootic paraplegia (''renguera''), or paralysis of the legs, a disease of lambs in the Peruvian Andes, by transferring some 50 *Melophagus ovinus* from sick to healthy animals. Boné (1939, p. 483) attempted to transmit the spirochete of African recurrent fever (*Treponema duttoni*) by feeding newly-emerged *Melophagus ovinus* on an infected mouse and injecting the ground fed keds in clean mice. The spirochete survived only 2 days in the insect; other experiments also showed that the keds are unable to transmit the spirochete by the bite.

In the discussion of the rickettsial parasites of the Hippoboscidae, I expressed the opinion that *Rickettsia melophagi* of *Melophagus ovinus* is not inoculated to sheep by the keds and is non-pathogenic. Giordano and Giordano (1935) considered the possible rôle in Tripoli of the dog-fly, *Hippobosca longipennis* (= *H. capensis*) in the transmission of Marseilles or "boutonneuse" fever (*Rickettsia conorii* Brumpt), a rickettsial disease of Man and animals, but offered no evidence that this insect was involved. Neitz (1937, p. 12), in South Africa, attempted to transmit eperythrozoonosis (caused by *Eperythrozoon ovis*) to healthy sheep made susceptible by splenectomy, by the intravenous injection of emulsified sheep-keds, *Melophagus ovinus,* collected from sheep infected with the disease, but he was unsuccessful. O'Roke (1936) suggested that the American deer-keds (*Lipoptena*) might be involved in the spread of sickle-cell anemia among deer. Baruchello and Mori (1907, *Centralbl. Bakt. Paras., Abt. 1, Orig.,* **43**, p. 602) intimated that piroplasmosis of horses (*Babesia caballi* or *B. equi*) might be transmitted in Italy by *Hippobosca equina,* but offered no proof; this disease is now recognized as being transmitted by ticks. Canham (1943, *Jl. South Afric. Vet. Med. Assoc.,* **14**, p. 85) suspected that a *Rickettsia*-like organism in the blood of domestic pigeons, in South Africa, might be transmitted by *Pseudolynchia canariensis* (= *P. maura*); but he was unable to find the organism in any of the flies.

Laveran (1902) and Theiler (1903) originally thought that *Trypanosoma theileri* Laveran was the causative agent of so-called "galziekte," a serious cattle disease in South Africa, and that the disease was transmitted by two species of *Hippobosca* (*H. rufipes* and *H. variegata* = *maculata*). Both conclusions were shown to be erroneous by Theiler's own later work. Galziekte is now believed to be caused by an intracellular micro-organism, *Anaplasma marginale* Theiler, transmitted by ticks. *Trypanosoma theileri* is recognized as an apparently innocuous blood parasite of cattle, world-wide in distribution and inoculated by tabanids (Nöller, 1916, *Berlin. Tierärztl. Wochenschr.,* **32**, pp. 457–460; 1925, *Centralbl. Bakt. Paras., Abt. 1, Referate,* **79**, pp. 133–142). The rôle of *Hippobosca,* even as an accidental, mechanical vector, cannot be of much importance, since the trypanosome is found in cattle in many regions, such as the New World, where this fly is unknown. The transmission of *Trypanosoma melophagium,* of domestic sheep, by

Melophagus ovinus, and of *T. theodori,* of domestic goats, by *Lipoptena capreoli,* was discussed in the section on the protozoal parasites of the flies; neither trypanosome is pathogenic to its vertebrate host. I have also mentioned Aragão's (1927) unsuccessful attempts to transmit *Trypanosoma hannae* of domestic pigeons by *Pseudolynchia canariensis.* Duke (1913, p. 57) reported that Dr. van Someren claimed to have transmitted a trypanosome of cattle by a species of *Hippobosca* in East Africa, but the evidence for this was never published. However, Baird (1931) was unsuccessful in attempts to transmit the common *Trypanosoma brucei* Plimmer and Bradford, of East African cattle, by the bite of *Hippobosca longipennis* (= *H. francilloni*).

Rodhain and Brutsaert (1935) describe interesting experiments in which they infected *Melophagus ovinus* with *Trypanosoma lewisi* (Kent), a common, non-pathogenic world-wide parasite of rats (normally transmitted by fleas), and with *Trypanosoma cruzi* Chagas, a parasite of various wild mammals in the New World, pathogenic to Man (normally transmitted by bugs of the subfamily Triatominae). Keds bred from puparia and fed on rats infected with *T. lewisi* or on guinea-pigs infected with *T. cruzi,* contracted permanent infections of the gut with these trypanosomes, which completed their cycle in the keds, producing eventually infective, so-called metacyclic forms in the hind-gut. When the contents of the hind-gut containing these metacyclic trypanosomes were injected in the peritoneum of clean rats or guinea-pigs, the animals became infected. These experiments are most interesting from a theoretical point of view, as showing the loose host-specificity of certain types of trypanosomes. They do not prove, however, that *M. ovinus* is to be incriminated as a natural vector of either *T. lewisi* or *T. cruzi,* since the keds never feed in nature on any of the wild mammals infected with these trypanosomes.

Leishmania, a genus of flagellates related to *Trypanosoma,* contains several species pathogenic to animals and Man. Gachet (1915, p. 480) observed, in Iran, that the dog-fly, *Hippobosca longipennis* (= *H. canina*), feeds sometimes at the edges of sores on dogs infected with Oriental sore (*Leishmania tropica;* "bouton d'Orient"). He claimed that *Leishmania* bodies occurred in the gut of some of these flies and also that two persons bitten by dog-flies later developed sores, in one case at the very locus of the bite. Gachet's observations have not been confirmed by rigorous experiments. It is most improbable that the dog-fly is a normal vector of *L. tropica,* which is transmitted regularly by species of *Phlebotomus,* or sand-flies. De

Paolis (1935, p. 184) inquired into the possibility of *Melophagus ovinus* being involved in the transmission of leishmaniasis of sheep and concluded that keds could not be incriminated. In discussing the Hippoboscidae attacking Man, I mentioned briefly the supposed connection of *Olfersia coriacea* with human cutaneous leishmaniasis in Central America. This disease, caused by the American strain of *Leishmania tropica* (sometimes differentiated as *L. brasiliensis*), is now generally believed to be transmitted by the bite of sand-flies (*Phlebotomus*), as is true for the Old World strain. It is common in the humid, densely forested areas of the Yucatan Peninsula (Quintana Roo and Campeche), British Honduras (Belize) and Guatemala (Peten). In Man, the sores occur as a rule on the exposed parts of the body, frequently on the ears. Various insects are blamed by the inhabitants of the infected regions. In Yucatan and northern Guatemala, the sores are usually attributed to the bite of *Olfersia coriacea,* a bird-fly frequently found on certain common gallinaceous game-birds, the crested curassow, *Crax rubra,* the bare-throated guan, *Penelope purpurascens,* and the chachalaca, *Ortalis vetula.* Some local medical authorities adhere to this view (Farfán y López, 1922; Beltrán, 1944; Fuentes Novella, 1944; see also J. Bequaert, 1933*a,* p. 570). At present there is no trustworthy experimental proof that the bite of *Olfersia coriacea* ever inoculates the disease. Moreover, it has not been shown that any of the game birds, which are the normal hosts of *O. coriacea,* are ever infected with *Leishmania.* They should be the reservoir of the disease if their bird-fly were the transmitter. Since several species of *Phlebotomus* are common in the area where the disease is prevalent, it is more probably spread by sand-flies in Central America, as elsewhere. While in Yucatan, Dr. R. A. Paynter, Jr., was particularly interested in the rumored connection of cutaneous leishmaniasis with *Olfersia coriacea,* locally known as ''mosca chiclero.'' Although he found the fly on many of the large game birds collected, it never did land on him. He was also unable to find a bird with sores. He informed me (*in litt.,* 1949) that he was most skeptical about bird-flies transmitting the disease.

Because birds are often infected with *Leucocytozoon* and *Haemoproteus,* blood parasites of the family Haemoproteidae, and because of the close association of certain hippoboscids with the infected birds, the flies have been repeatedly suspected of transmitting these Protozoa (Nöller, 1920, p. 167; and others). Wülker (1925*a;* 1925*b;* 1926, p. 214) asserted that a *Leucocytozoon,* common in crows in Germany, was transmitted by *Ornithomyia avicularia,* but gave no experimental proof of his contention. Up to the present, it has not been shown that hippoboscids act as vectors of any *Leucocytozoon;* but it has been definitely proved that two species, *L. simondi* of ducks and *L. smithi* of turkeys, are transmitted by black-flies (Simuliidae). It may be pertinent to note in this connection that infections of *Leucocytozoon* are usually much rarer in birds than those of *Haemoproteus.* For instance, Huff (1939) found in the United States infections with hematozoa in 32 species of birds, mostly song birds and doves. No infections were found in 545 birds; 324 were infected with *Haemoproteus,* 59 with *Plasmodium,* 11 with *Trypanosoma,* and 11 with *Leucocytozoon.* If Hippoboscidae were the vectors of both *Haemoproteus* and *Leucocytozoon,* one might expect these parasites to be about equally frequent in the birds.

The regular transmission by Hippoboscidae of several of the *Haemoproteus* of birds is much more probable, since there is now positive proof of this for *H. columbae* Kruse of domestic pigeons and *H. lophortyx* O'Roke of California quail.

The generic name *Haemoproteus* and the trivial name *columbae* were first used in print by Kruse (1890, p. 370) for a blood parasite of the domestic pigeon, of which a rather confused account had been published shortly before by Grassi and Feletti (1890, p. 4). Celli and Sanfelice (1891*a*, pp. 43–46, pl. 2, figs. 1–15; and p. 61, where Kruse's name is adopted; 1891*b*, pp. 507–510, pl. 17, figs. 1–21, without generic or specific name) gave the first complete description and recognizable figures of this parasite. This may be why Wenyon (1926, **2**, p. 888) and others credit the name to Celli and Sanfelice. *H. columbae* causes in domestic pigeons a serious and widespread disease, now recognized in southern Europe, Africa (Algeria, Tunis, Portuguese Guinea, Angola, Belgian Congo, South Africa, etc.), India, Hawaii, most of the United States (except the northern states), Mexico, Colombia, Venezuela, Brazil, Uruguay, and Argentina. It occurs probably wherever pigeons are infested with their specific fly, *Pseudolynchia canariensis* (= *Lynchia maura;* other synonyms in a previous section on the protozoan parasites). That the pigeon-fly is the regular vector of *H. columbae* was proved conclusively by Edm. and Et. Sergent (1906; 1907). Their experimental work is a model of the kind and for this reason will be considered more fully. Some of the experiments were carried out at Algiers, where the local pigeons are generally infected, so that clean birds had to be imported from northern France; others were made at Paris, where both the fly and the blood parasite do not occur, infected pigeons being then brought from North Africa. The experiments were many and varied, and in every case clean pigeons were kept as controls in the same room, but in screened cages away from flies. Only a few of them are summarized here; but all should be carefully studied by would-be workers in this field. In a first experiment, 3 clean Paris pigeons imported to Algiers were placed in separate cages on August 20, one alone, the second with a heavily infected local pigeon free of flies, and the third with a heavily infected local pigeon carrying some 15 *Pseudolynchia canariensis.* On October 8, the Paris pigeon in the cage with the infected pigeon and the flies, showed the first *Haemoproteus* in the blood; the Paris pigeons in the other two cages never became infected. In another experiment, 3 Paris pigeons, kept isolated in a screened cage since early February, received, about the middle of May, 11 *P. canariensis* removed from infected Algerian pigeons; these Paris pigeons showed infections on June 14, June 25 and July 9 respectively. On November 14, 2 infected Algerian pigeons with many flies were carried from Algiers to Paris in a screened cage together with a clean Paris pigeon, the infected birds being separated from the healthy one by a partly open partition; the infected pigeons died on the way and were deserted by the flies for the clean bird, which showed a *Haemoproteus* infection on January 23. Infection of a clean pigeon with the disease was attempted by feeding it by mouth 33 live *P. canariensis* taken from infected pigeons, but the clean bird never became infected; from which it was concluded that the parasite is inoculated by the bite of the fly. In another experiment, flies bred from 17 puparia produced by flies which were certainly infected, were placed on a clean Paris pigeon, which never became infected, showing that the *Haemoproteus* is not transmitted by an infected female fly to her offspring.

The Sergents found that in bred *P. canariensis* fed on infected pigeons, the parasites ingested with the blood eventually produced in the fly's mid-gut forms which they regarded as oökinetes. They were unable to trace any further development of these in the fly or to determine the infective form inoculated by the bite to the pigeon. Similar results were obtained by Aragão (1907; 1908; 1916), in Brazil, and by Gonder (1915*a;* 1915*b*), in South Africa, both of whom used *P. canariensis* (recorded under various synonyms). Gonder concluded that *Haemoproteus columbae* never develops beyond the oökinete stage in the fly's gut and he even claimed that infected flies lose their infectivity when they feed upon healthy pigeons. Coatney and Hickman (1952), in the United States, also infected healthy domestic pigeons both by the bite of infected *Pseudolynchia canariensis* and by the intramuscular injection of infected salivary glands of the fly.

Helen Adie (1915; 1924; 1925) described what she regarded as the oöcysts of *H. columbae* in the wall of the mid-gut, as well as sporozoites in the salivary glands of *P. canariensis.* These interpretations were accepted by Aragão (1927) and Wenyon (1926, **2**, pp. 894–896; figs. 383 and 386). If they are correct, the various stages of development of *H. columbae* in the pigeon-fly would correspond closely with those of true malarial parasites (*Plasmodium*) in mosquitoes and be as follows. The asexual cycle or schizogony in the pigeon eventually produces male and female gametocytes in the blood-corpuscles. When infected blood enters the gut of the pigeon-fly, the male gametocyte produces male gametes by active flagellation; the female gametocyte develops into a single female gamete, which, after impregnation by one of the male gametes, gives rise to a motile zygote or oökinete. This oökinete penetrates the wall of the hind portion of the mid-gut and produces on its outer surface pigmented oöcysts, which project in the general body cavity. The oöcysts grow and when mature measure about 26 μ in diameter; they give rise to many sporozoites, each up to 10 μ long. Eventually the sporozoites are found in the salivary glands, which in infected flies are sometimes packed with them. Adie did not describe how the sporozoites reach the salivary glands after the mature oöcyst releases them by rupture. Although Aragão (1927) confirmed Adie's observations, he noted that in his experiments the oöcysts and sporozoites were not as numerous in infected flies as Adie had found them and that their scarcity was out of proportion to the numerous zygotes seen in the lumen of the gut. Aragão also stated that he infected clean pigeons by injecting emulsions of bred flies 120 hours, or the 5th day, after feeding the flies on infected pigeons. Kartman (1949, p. 131, figs. 3A–B) recently described and figured structures protruding from the outer wall of the mid- and hind-gut of *Pseudolynchia canariensis,* in Hawaii, which he interprets as the oöcysts of *H. columbae,* in accordance with Adie's and Wenyon's views.

Although Wenyon states that there is no longer any doubt about the cycle described by Adie being correct, certain features of it do not seem to be satisfactory. There remains an unknown gap between the sporozoites supposedly produced in the oöcysts in the wall of the mid-gut and those that are said to be infective in the salivary glands. The scarcity of the oöcysts, to which Aragão (1927) called attention, is rather disturbing. In a recent conversation, Dr. Coatney, who carried on extensive experiments with *H. columbae* and pigeon-flies, informed me that he has misgivings about some of the details of the cycle described by Adie and Wenyon. In particular, he was never able to observe the protruding oöcysts on the wall of the mid-gut in flies which were unquestionably infected. As Dr. Coatney also pointed out, it is entirely possible that the sporogony of *H. columbae* in the fly might be very much like or identical to that of the closely related genus *Leucocytozoon.* According to recent work by Fallis, Davies and Vickers (1951), the sporogony of *Leucocytozoon simondi* of ducks is completed in the lumen of the gut of black-flies, its regular vectors. These workers were unable to demonstrate oöcysts on the outer wall of the gut, but found fully-developed oöcysts as well as sporozoites among the gut contents. As sporozoites could not be located clearly inside the salivary glands of infected black-flies, it is possible that they travel directly from the gut into the blood stream of the duck when the infected fly feeds. It appears, therefore, that further research is called for to determine to what extent the production of oöcysts in the wall of the mid-gut of the pigeon-fly is a normal and essential feature of the sporogony of *H. columbae.*

Coatney (1933), in North America, was unable to transmit *Haemoproteus columbae* from the domestic pigeon to the mourning dove, *Zenaidura macroura carolinensis,* by *Pseudolynchia canariensis.* Kartman (1949, pp. 128–129), in Hawaii, was also unsuccessful in similar attempts to infect the Chinese dove, *Streptopelia chinensis,* the ring-neck dove, *S. decaocto,* the barred dove, *Geopelia s. striata,* as well as domestic fowl.

On the other hand, Huff (1932) succeeded in transmitting two species of *Haemoproteus* normally found in *Zenaidura macroura carolinensis, H. sacharovi* Novy and MacNeal and *H. maccallumi* Novy and MacNeal, from the dove to the domestic pigeon by newly-bred *Pseudolynchia canariensis.* This fly has not been found thus far on American wild Columbidae, which, however, are known as regular hosts of some other, native hippoboscids. Both *Microlynchia pusilla* and *Stilbometopa podopostyla* were reported from the American mourning dove by Coatney (1938) and Brennan

(1938).[31] *M. pusilla* seems to be widespread on this host, as I have records from California, Idaho, Iowa, Nebraska and Texas; most probably it is the natural vector of the two *Haemoproteus* of mourning doves. Huff (1939, p. 619) concluded that "natural transmission of the *Haemoproteus* infections of doves by hippoboscids remains the best hypothesis."

Transmission experiments with *Haemoproteus columbae* and various arthropods other than *P. canariensis* may be mentioned briefly because of their possible bearing on the problem of the sporogony of this parasite. Aragão (1916) saw the formation of oökinetes in the gut of a mite (*Dermanyssus*) and of 3 Brazilian species of mosquitoes. Nöller (1920, p. 152) obtained the development to the oökinete stage in the gut of the bed-bug, *Cimex lectularius.* Neither Aragão nor Nöller were able to infect the pigeon with the oökinetes produced in these unusual arthropods.[32] Rivero (1947), in Mexico, described the formation of oökinetes of *H. columbae* in the gut of a blood-sucking reduviid, *Triatoma rubida* Uhler, fed on an infected pigeon. It occurred within 24 hours after the infective meal; but degeneration had set in at 72 hours and no oökinetes remained at later examinations. He stated that he infected healthy pigeons by injecting them in the veins with the gut contents of the infected *Triatoma,* 24, 48 or 72 hours after the infective meal. Contrary to the foregoing observations, Kartman (1949), in Hawaii, failed to observe the formation of oökinetes in the gut of two mosquitoes, *Culex quinquefasciatus* and *Aëdes albopictus,* and of a hippoboscid from Oceanic birds, *Olfersia aenescens,* allowed to feed on infected pigeons.

Haemoproteus lophortyx O'Roke (1929*a*) is a common blood parasite of California quail, *Lophortyx californica,* in which it causes a disease, varying from chronic to acute or fatal according as to whether the infection is either mild or heavy. It is assumed that in chronic cases the quail remain infected for life, the longest duration of an infection observed in captivity being over 4 years and 8 months (Herman and Bischoff, 1949, p. 295). As far as known, the only vectors in nature are the two common and specific hippoboscids of quail, *Lynchia hirsuta* and *Stilbometopa impressa.* The sporogony of the parasite in the flies is very incompletely known, in spite of the work of O'Roke (1929*b;* 1930; 1932; 1933). Eight of his experiments, in which *L. hirsuta,* taken from infected quail, were allowed to feed on young, hatched, uninfected quail, gave negative results. His only positive experiment was by injecting a young clean quail intramuscularly with the salivary glands and part of the gut, macerated in normal saline, of an infected fly taken from a wild infected quail. The infection appeared 27 days later, but was very light and lasted only 9 or 10 days, after which it disappeared spontaneously, the bird never showing symptoms of disease. O'Roke (1930, p. 31) observed the gametocytes and oökinetes in the gut of *L. hirsuta* captured on an infected quail. He described the penetration of the oökinete into the wall of the gut as follows: "Among whole and partly digested red blood cells were a number of rounded gametocytes, whose sex could not be determined, together with three oökinetes. Two of these were inactive, but the third was apparently just attaching itself to the inner wall of the gut. To permit continued observation the edge of the cover slip was then sealed. Ever so slowly, the forward end of the oökinete penetrated the wall, whether intercellularly or intracellularly could not be determined. It is interesting to note that the narrower, more transparent end of the oökinete entered the wall of the gut first. . . . In about 50 minutes the posterior end of the oökinete had disappeared from the lumen of the gut. Seventy minutes later a tiny swelling appeared just beneath the outer membrane of the gut, and because of its greater opacity was believed to represent the earliest formation of an oöcyst. No further change occurred, and 6 hours later all the tissues were dead and transparent." O'Roke also described and figured what he regarded as the sporogony stages of *H. lophortyx,* using oökinetes, oöcysts and sporozoites found in some wild *L. hirsuta,* taken from infected quail. He noted that the flies were never heavily infected, the greatest number of oöcysts found in one fly being 11, only 4 of which were mature.

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[31] Herman's (1937) record of *Ornithoica vicina* (= *confluenta* of authors) from trapped mourning doves on Cape Cod, Massachusetts, must be discarded as most probably due to live contamination in the traps.

[32] Wenyon (1926, **3**, p. 897) makes it appear as if Nöller also used mites, fleas and *Aëdes aegypti* in transmission experiments with *H. columbae.* Such is not the case, however.

According to Herman and Bischoff (1949, p. 293), Kadner observed in 1941 developmental stages of *Haemoproteus lophortyx* in *Stilbometopa impressa,* but did not transmit the infection to quail by this fly. The details of this work were never published. Herman and Bischoff (1949, p. 295) also found sporozoites in the salivary glands and body cavity of a *S. impressa* taken from a heavily infected wild quail. Material including the salivary glands macerated in normal saline was inoculated into the breast muscle of an immature quail showing no parasites in the blood and coming from an area in San Francisco where trapped quail never had been found infected with *Haemoproteus.* This bird showed parasites in the blood 21 days after the inoculation and died of the infection 10 days later. Recent unpublished investigations by I. B. Tarshis prove that *S. impressa* transmits *H. lophortyx* to quail by the bite.

Herms and Kadner (1936; 1937) claimed to have shown by experiments that *Lynchia fusca,* a common fly of owls and occasionally of hawks in California, is capable of transmitting *Haemoproteus lophortyx* from quail to quail. Their work is by no means conclusive. Since *L. fusca* has never been taken on quail, it could scarcely be involved in the transmission of *H. lophortyx* in nature. On the other hand, *L. hirsuta* does not occur on owls or hawks, so that it could not well infect these birds with the blood parasite of quail. Herman (1945, p. 22) suggested that *L. fusca* might be the vector of the species of *Haemoproteus* found in owls and hawks, but offered no experimental proof.

McMurrich (1884), Flattely (1922) and Jenkins (1924) considered the possibility of the sheep-ked, *Melophagus ovinus,* being the intermediate host of the sheep tape-worm, *Moniezia expansa* (Rudolphi). But this could not be proved experimentally and, in recent years, Stunkard (1938, *Parasitology,* **30**, pp. 491–501, 1 Pl.) has shown that certain oribatid mites act as intermediary hosts of this worm.

Control Measures. The control of the Hippoboscidae is only called for in case of heavy infestations of domestic animals. It is easily carried out with the modern insecticides. A great choice of these is now available. A recent book by A. W. A. Brown (1951) reviews the whole subject and gives the technical names and chemistry of the several products that have been recommended.

Pseudolynchia canariensis. The control of the pigeon-fly is discussed in detail by F. C. Bishopp (1929*a;* 1929*b;* 1929*c;* 1942). Pyrethrum powder or rotenone dusted in the feathers, particularly the downy areas near the skin, will kill the flies on adult pigeons. Recently, Yager and Gleiser (1946) found that talcum powder containing 10 per cent of DDT, dusted in the feathers at the rate of 3 gm. per bird, kills all the flies within 24 hours. As the puparia occur away from the hosts, they may be removed with the refuse from the floor of the loft and burned. All cracks of the floor and walls should be cleaned and washed with kerosene. In the northern United States the pigeon-fly is scarcely ever a pest; but it may be imported sometimes with birds from farther south and become established during the summer months.

Melophagus ovinus. Many papers have been published on the control of the sheep-ked and most of these have been listed in the Bibliography. It is probably the most easily controlled louse-fly, since both the adults and the puparia can be dealt with in the fleece. In some countries control of keds by dipping in liquid insecticides has been made compulsory by law. Until recently, the dips most often used were coal-tar-creosote, cresol, nicotin, or lime-sulphur-arsenic. As these could not be depended upon to kill all adults and puparia at one dipping, the operation had to be repeated every 24 to 28 days. These methods are now superseded by the use of more modern chemicals. Graham and Scott (1948), in Australia, made a critical study of the relative value of several insecticides against the sheep-ked. They found that arsenical dips were of little value. Rotenone is very toxic to adult keds, but not lethal to the puparia and leaves not enough lasting toxicity in the fleece to kill all adults emerging from remaining puparia. In suitable concentrations, DDT and BHC (benzene hexachloride) should both prove highly effective for the eradication of sheep-keds. They kill all adults rapidly and the fleece remains toxic long enough to kill those escaping from surviving puparia. When dipping with these chemicals is carried out properly, sheep may remain free of keds in a flock for a month or more. According to H. Shaw (1946), the effect of DDT on keds is even more spectacular than that on ticks. Slade (1945) and Steward (1946) recommend gammexane, an isomer of benzene hexachloride, for the control of keds. Schwardt and Matthysse (1948) discuss at length the materials and equipment needed.

No work seems to have been done on the control of the goat-ked, *Lipoptena capreoli,* possibly because it is of little economic importance. Eads (1949), in Texas, obtained excellent results in cleaning deer in captivity of *Lipoptena mazamae* by spraying with 1 to 2 per cent wettable DDT in one U. S. pint (0.47 liter) per animal.

Hippobosca equina. Savik (1950) found benzene hexachloride highly effective against louse-flies on horses.

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